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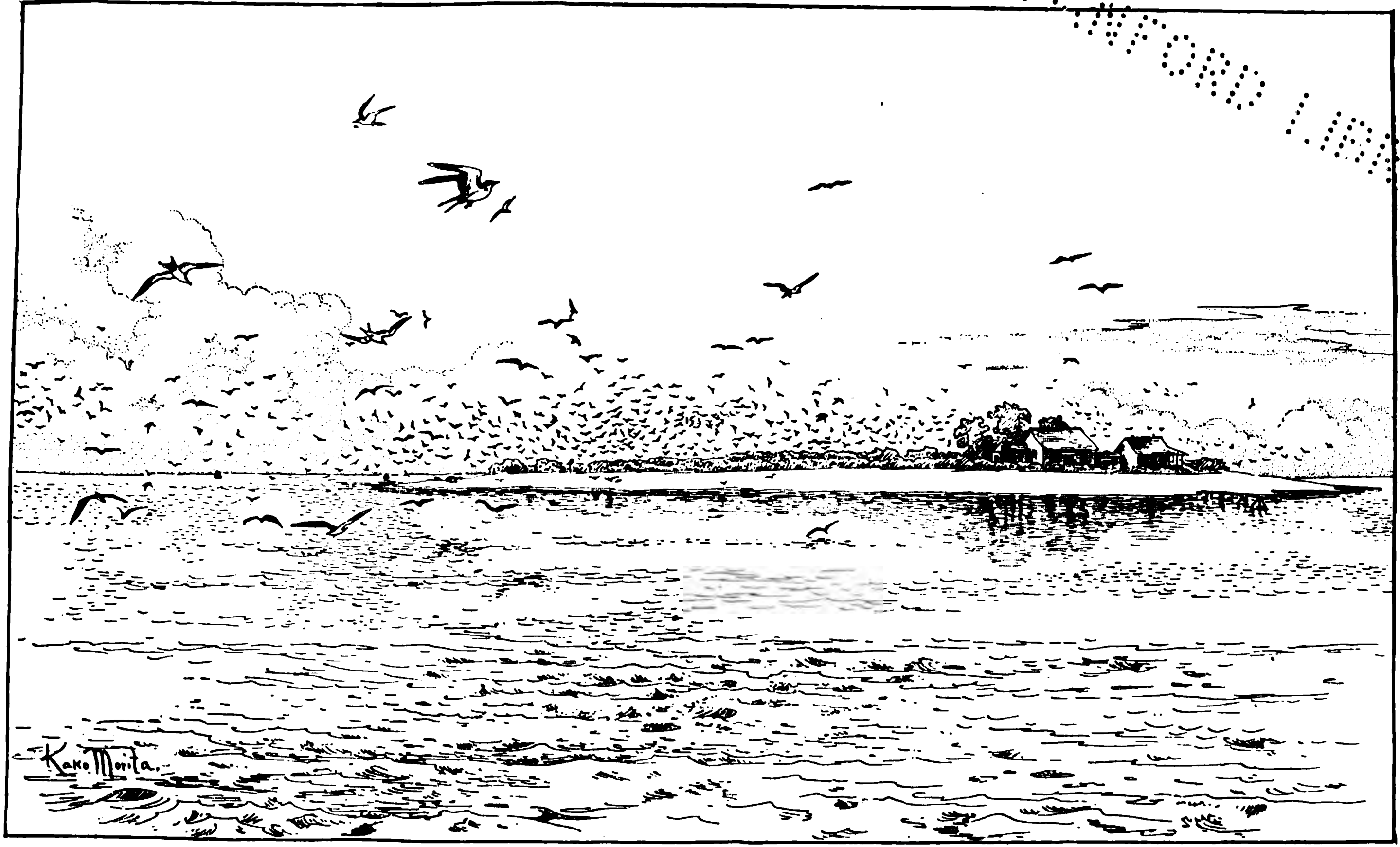

Bird Key viewed from the West, showing certain topographical features of the Key.

PAPERS FROM THE DEPARTMENT OF MARINE BIOLOGY
OF THE CARNEGIE INSTITUTION OF WASHINGTON
ALFRED G. MAYER, DIRECTOR

VOLUME VII.

HOMING AND RELATED ACTIVITIES OF BIRDS

BY J. B. WATSON AND K. S. LASHLEY

THE ACQUISITION OF SKILL IN ARCHERY

BY K. S. LASHLEY

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PREFACE.

The present series of studies on the behavior of birds is a direct outgrowth of an investigation made on the noddy and sooty terns nesting on Bird Key, Tortugas, Florida, by the writer under the auspices of the Marine Biological Laboratory of the Carnegie Institution of Washington in 1907 (publication 103). The homing "instinct" is the central topic in all the papers. In the 1907 investigation the fact appeared that terns possess a homing sense, behaving exactly as do homing pigeons when sent away from their nests and young. Such good subjects did the terns appear to be that it was soon decided to make this homing sense the chief object of the Tortugas researches. The topographical situation of Bird Key makes that island especially suitable for carrying out such experiments. In the first place, it is the northern limit of migration of these tropical birds. It becomes possible there to test whether the birds can home in a region never before, in all probability, visited by them. This can be accomplished by sending the birds anywhere north of Bird Key. Secondly, on account of the fact that Bird Key is the last body of land between the coast of Florida and the coast of Texas, the birds can be sent out for hundreds of miles over open water. There is thus afforded an opportunity for testing homing where apparently no "visual landmarks" can exist. These two conditions have never before been realized, and they are conditions which are indispensable in even a preliminary scientific study of homing.

The 1907 investigation already referred to is concerned largely with instincts in terns—those of feeding, nesting, brooding, etc. It was necessary to have some survey made of these instinctive types of behavior before the homing instinct itself could be investigated. A part of the opening paper, pp. 35–45, in the present series gives much additional data on the nesting activities which have a bearing upon the control of experiments on homing. These observations are concerned with the instincts connected with the brooding of the egg, such as the number of shifts at the nest; retention of mate and nest habits; water habits and instincts, etc. It is thought that these observations, when taken in connection with those made in the first study, afford accurate means of testing the homing ability in these two species of terns.

Having made the necessary investigation of the instinctive life of the terns, it became possible to carry out homing experiments. Preliminary experiments in 1910 (p. 47) showed clearly that in order to make a success of the work, some well-trained investigator would have to be sent out with the birds. In the 1910 work the terns were sent out with responsible men attached to the laboratory but who had had no training in feeding and caring for them. On account of this, usually something like half of the birds died *en route*, and the rest were released at the more distant points in very poor condition. In order to meet this difficulty, Dr. K. S. Lashley was asked in 1913 to associate himself with the work. The very successful returns from the second Galveston trip (p. 54) are due largely to his care of the birds on the forward journey.

In addition to his invaluable aid in the problem of distant orientation, Dr. Lashley separately began a study of *proximate orientation* (p. 61), *i. e.*, of the behavior of the terns in locating the nests, mates, young, etc. This paper, in addition to supplementing the work on distant orientation, opens up a wealth of new problems on bird activities in general, and furnishes methods which may acquire a usefulness much wider than their present connections.

Our experiments and conclusions on homing proper will be found on pages 59 and 60. These results, while not settling the question of the sensory mechanism by means of which the birds return to the nests, *do remove all doubts about the fact that the noddy and sooty terns can return from distances up to 1,000 miles in the absence of all landmarks* (at least in so far as the term landmark is understood at present). The problem of homing has thus become defined, and experimental work of a definite kind is needed for its solution. The paper on vision in birds (p. 87) seeks to gain some insight into the question as to whether the birds have any special visual equipment (such as infra-human sensibility to rays of light, sensitivity to infra-luminous rays, etc.) which might be employed by them in finding their goal. This paper marks only the beginning of the research into the sensory mechanism possibly used by birds in homing. So far we have not been able to locate the sensory factors used in return, but we are far from being without hope that future studies may yield results which will enable us to solve the riddle which has been propounded to scientific men of all ages, but as yet never satisfactorily answered.

The final paper by Dr. Lashley, on the acquisition of skill in archery, has of course no connection with the work on homing. Its inclusion in the present volume is made desirable by the fact that the work was begun at Tortugas under the same arrangements that were made for the other investigations.

Both Dr. Lashley and I wish to express our thanks to Dr. A. G. Mayer, Director of the Marine Biological Laboratory, for his generous assistance in these investigations.

JOHN B. WATSON.

THE JOHNS HOPKINS UNIVERSITY,
February 1915.

AN HISTORICAL AND EXPERIMENTAL STUDY OF HOMING.

BY JOHN B. WATSON,
Professor of Experimental and Comparative Psychology at the Johns Hopkins University,

AND

√ K. S. LASHLEY,
Johnston Scholar in Psychology at the Johns Hopkins University.

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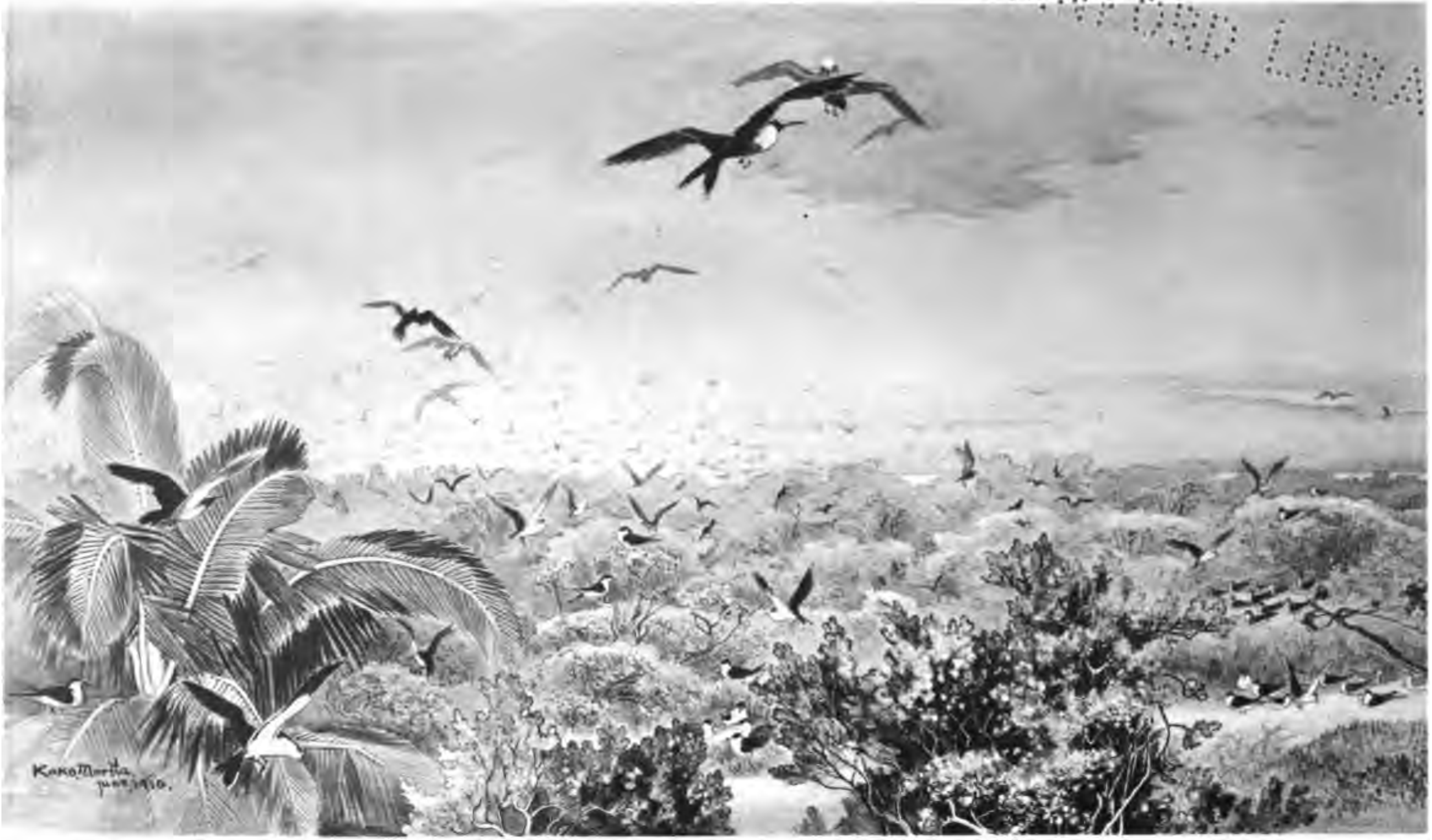

A VIEW OF BIRD KEY BEFORE THE HURRICANE OF 1910 DESTROYED THE BAY CEDAR BUSHES.

AN HISTORICAL AND EXPERIMENTAL STUDY OF HOMING.

INTRODUCTION.

In 1907, while the senior author was making a study of the nesting behavior of the noddy and sooty terns at Bird Key, Tortugas, Florida,* the fact was observed that these birds possess a well-developed homing "sense." Only a few experiments were made at that time (see p. 46), but the results were so promising that Dr. Alfred G. Mayer, Director of the Marine Biological Station of the Carnegie Institution of Washington, made special arrangements for the continuation of the work in 1910, 1912, and 1913. Since the homing season is only 5 to 6 weeks in length (being limited to the laying and brooding periods), the present summary of the three years' work is far from being satisfactory. Notwithstanding our failure to work out completely the problems of homing in the terns, we feel that we have made so many improvements in our technique—in the matter of caring for the birds on trips, locating them on return, etc., that it is advisable to report both what we have on homing and on the control of homing experiments. Some care has been taken in the present investigation to supplement the 1907 work on the instinctive life of the terns. This was found to be desirable in view of the fact that in the control of the experiments on homing it becomes essential to have some accurate data on the ability of the birds to swim and to remain on the water at night; the length of time the nesting impulse remains strong; the length of time habits of reacting to one nest and to one mate are retained, etc. The actual experimental material on distant orientation will be given in detail, but the observations upon the instincts and habits of the birds will be presented in a more or less abridged form.

On pages 34 and 35 we give the location of Bird Key, a description of the colony of terns dwelling there, and the complete setting of our experimental work.

Before presenting our own work we shall give in some detail the general historical setting of the problem of homing in vertebrates.

HISTORICAL OUTLINE OF THE PROBLEM OF HOMING.

According to Exner† the problem of homing is a very ancient one. The earliest mention of the use of the homing pigeon is found in the writings of Anacreon (born 550 B. C.). The pigeon post as an institution reached probably its highest degree of development in the reign of the Caliphs—in the year 1200 A. D. For hundreds of years the whole of Persia, Servia, and Egypt was covered with pigeon côtes owned by the government, and attached to each was the official post-office and the official postmaster. That the Crusaders used pigeons to transmit messages to their friends and relatives is also well known.

Probably the use of these birds in times of war, and especially in besieged fortresses, is best known. So important was their use in this respect that until 1850 almost every army post and fort had its côte and was supplied with pigeons from other military fortresses. Indeed, the French extended the use of the homing pigeon to the field by equipping the côtes with wheels (traveling côtes) and training the birds to return to these rolling habitations regardless of their location. They further extended the use of the homing pigeon by establishing côtes on board war vessels. The commercial value of the pigeon post has been very great indeed. Practically all of the boards of trade in the large cities of Europe were once supplied with homing pigeons. Their use in obtaining advance information concerning crops, local insurrections, rumors of war, etc., can hardly be overestimated. Newspapers likewise were supplied with such pigeon posts. A rather lengthy dispatch could be sent, when it is remembered that the message, after it was written, could be micro-photographed in such a way that 50,000 words could be contained on a paper which had a weight of less than 0.5 gram. The dispatch could then be read under the microscope by the receiver.

---

*John B. Watson: "The Behavior of Noddy and Sooty Terns." Carnegie Inst. Wash. Pub. 103, p. 189.

†"Das Räthsel der Brieftauben," Wien. 1892.

The decline of the usefulness of the pigeon dates back to the establishment of the telegraph and field telephone lines, and on sea to wireless telegraphy. Even in the present European war, if reports may be trusted, the birds are used to some extent in the scouting work of the balloon and aeroplane corps.

Claparède* has given a very brief description of the theories of homing and of the problems in homing. The theories he classifies as follows:

1. *Magnetic Sense* (Viguier-Caustier?).†
2. *Atmospheric Currents, Winds*, etc. (Toussenel, Ziegler?).
   "*Ideas of the Atmosphere*" (Thauzies?); *Special Nasal Sense* (Cyon).
3. *Direction of the Sun, of Light* (Romanes, Lubbock, Wasmann).
4. *Special Force* (Fabre); *Attraction of Purely Reflex Origin* (Netter, Bethe); *Tropism* (Loeb).
5. *Registration of Detours* (Darwin, L. Morgan); *Contrepied* (Reynaud, P. Bonnier).
6. *Points de Repère, Topographical Memory* (Wallace, Romanes, Lubbock, Forel, Fabre, Wasmann, Yung, Bouvier, Marchal, Marchand, Buttel-Reepen, Peckham, Rodenbach, Ziegler).
7. *Direct Perception of Goal* (Hachet-Souplet, Duchâtel); *Telepathy* (Duchâtel).
8. *Complex Phenomena Resting upon Intelligence* (Cyon).
9. *Hereditary Topographical Memory* (Kingsley, Parker and Newton).

Claparède classifies the various problems in homing as follows:

- Goal
  - Already known
    - I. Perceptible.
    - Non-perceptible
      - II. Where landmarks are at hand.
      - III. With no apparent landmarks at hand.
  - Unknown
    - IV. Perceptible.
    - Non-perceptible
      - V. Where intermediary stimulations are at hand.
      - VI. With no intermediate excitations.

---

*Archives de Psychologie, II, 1906, p. 133.

†Where an author is hard to classify an interrogation point is placed after his name. In many cases a given author makes use of more than one theory to account for the different phenomena of homing. Many authors whose names appear in the above lists are not again mentioned in this report. Reference to their work may be found in Claparède's bibliography. This bibliography, which is fairly complete up to 1906, is not duplicated here. Many references supplementary to our own are to be found in it.

It will be seen from this table that Claparède's treatment is far too broad to be of particular service to us in discussing the narrow division of the field of orientation which especially interests us in the present paper. Claparède includes in his discussion both vertebrates and invertebrates, both proximate orientation and distant orientation, and includes under the latter term all of the phenomena of migration. In our historical summary we shall deal with homing in *vertebrates* where the *goal is "already known."* At the outset it seems best to divide the subject of homing into two parts: (*a*) proximate orientation and (*b*) distant orientation.

PROXIMATE ORIENTATION.

The term proximate orientation ought to be understood as referring to the process of finding the goal (since we are in need of some general term covering nest, burrow, côte, etc., it seems well to let the word goal refer to any of these) when the goal itself directly and immediately stimulates the receptors of the animal. In other words, in proximate orientation vision, olfaction, audition, or some other distance receptor is being immediately stimulated by the goal. We might illustrate the process of proximate orientation by citing the case of the young bird which does not go out of sight of the goal to feed, and of young mammals which stay within call of the parent. It might be equally well illustrated in cases of animals with keen smell, which apparently can journey quite a distance away from the goal and still return to it by reason of the olfactory stimuli which emanate from it.

An interesting case of proximate orientation occurs thousands of times in the course of a single evening on Bird Key. As has been mentioned, the sooty tern often flies around the island at night. When it is remembered that the island is quite small, that there are probably 30,000 sooties there, and that they nest oftentimes not more than 10 inches apart, the problem of their return at night after these short journeys becomes a puzzling one. As a matter of fact, the bird hovers over the nesting area giving out his call; he is answered by his mate and young and is thus guided to the nest, often on dark nights. In this paper, then, proximate orientation will refer to those cases where orientation is effected through the action of a stimulus which emanates from the nest (sound, light, olfactory particles, etc.).*

DISTANT ORIENTATION.

Distant orientation involves always a return to the goal from a distance too great for the goal itself to function as a direct stimulus to any known receptor of the animal. It is obvious that the return in such cases can be effected only in one of two ways: (1) the animal may be guided back by a series of landmarks to which it has already established reactions (*points de repère*, "visual landmarks," "familiar landmarks," etc.). Such landmarks may appeal to any sense-organ possessed by the animal. If it is keen-sighted, we may suppose that the landmarks would be visual; if highly sensitive to olfactory stimuli, olfactory, etc. Those who support the landmark theory of homing usually suppose that there is a series or chain of such stimuli so placed that before one stimulus ceases to act another presents itself. It is obvious that the animal reacts to each of these serial landmarks as it would react to the goal itself. An obvious logical implication is that the animal—granted that it moves about at random until the first of these landmarks is reached—must be able to follow these clues in the direction towards the goal and not in the reverse way (in the case of a dog, *e. g.*, there must be no back-tracking). Were this not the case, the animal, approaching the chain of landmarks at right angles, by turning, *e. g.*, to the right, would meet a series which, if followed up, would take it home; if to the left, a series which would lead it still farther afield. We can conceive, under this hypothesis, of an animal being effectually lost in a wilderness of landmarks. In other words, if orientation is obtained by reference to landmarks, the trail must be polarized. It is also obvious that this hypothesis calls, first, for the ability on the part of the bird to form habits of very great complexity; second, that it must form them with extreme rapidity to account for the facts of homing (even in cases where landmarks are possible). For convenience we shall group all such theories under the heading of "habit theories of return." Such theories are advanced by Hachet-Souplet, Hodge, and others.

---

*On certain phases of proximate orientation, see Lashley, page 61 of this volume.

It is clear that if it can be proven that birds can return only over stretches which afford landmarks, then there is no real problem of distant orientation at all. The problem simplifies itself to the determination of what sense-organs the animal employs in its normal habits of reacting to objects, the intensity of the stimuli which call out such habits, and the rapidity with which such habits are laid down, etc. In essence, the problem is as simple as determining whether a young animal goes to its nest by reason of the presence of an auditory stimulus (cry of the parent) or through vision (sight of the nest); or gets out of the way of a hawk through the sight of the hawk or its shadow, or through the auditory stimulus set up by the crying of its neighbors.

On the other hand, the animal conceivably may be guided back reflexly through the action of some unknown intra-organic or extra-organic stimulus, acting upon some assumed but unknown sense-organ. We will call this hypothesis (2). We shall develop this conception in connection with the "contrepied theory" of Reynaud, the attitude theory of Bonnier, and the magnetic sense of Viguier and Thauzies, etc. In such reflex returns no special locality or position habits have to be formed. No landmarks are needed. All such theories we shall group under the heading of "reflex theories of return."

In the historical sketch which follows we have not tried to do justice to all theories nor to all experimental data. We have tried to present the more important theories and where possible some of the experimental details upon which they are grounded. We have spent a disproportionate amount of time upon the historical aspect of homing in vertebrates because no one hitherto has attempted to treat the subject in monographic form.

HABIT THEORIES.

THEORIES AND EXPERIMENTS ON THE FUNCTION OF VISION IN HOMING.

Hachet-Souplet* advances some positive proof that vision furnishes the data for distant orientation. He has made a number of experiments with traveling côtes. These traveling côtes are used quite commonly in France and in Belgium. We give here his account of some recent experiments:

> After having put in a basket and left at a point (A) a part of the inhabitants of the traveling côte, the exterior aspect of which was known to the birds, we sent the carriage forward to a distance of about 5 km. from the point A. The pigeons, released as soon as the carriage arrived at B, found it very rapidly. We have repeatedly tested this, increasing the distance from A to B up to 10 km. We have found it necessary to place the carriage, which is supplied with a large drapery, in an open territory. The birds have always found it. If this distance of 10 km. is passed we begin to undergo losses of the birds, and we have never obtained returns beyond the distance of 12 km. It is necessary to consider here that the birds know nothing of the *entourage* of their côte. If, proceeding otherwise, we make the carriage stationary on its arrival at the new place and allow the birds to reconnoiter the immediate environs before placing them in the basket (in accomplishing this we attach the birds to the carriage by cords which allow them to fly up to a height of 35 m.; in order to avoid accidents one attaches only two birds at a time) we have been able to obtain on the first attempt, without preliminary training, a return of 100 km. This was accomplished by 8 pigeons. At the time this test was made we had sent to the same point of release (100 km.) 10 pigeons which had been brought in the caravan without being allowed to leave it (that is, they were not allowed preliminary observation). All 10 of the birds were lost. This experiment was repeated with the same result several times.

Hachet-Souplet supposes that the view from the carriage supplied the birds with a set of "visual memories" which they could utilize—*i. e.*, that orientation is effected through sight. With regard to the limits within which a bird can return through direct sight he states that the limit is much further than it is at present believed to be. He considers what he calls the "law of the diminution of the necessary intensity of the excitant which determines the reaction." (He has in mind here, of course, decrease in the intensity, etc., of the visual stimulus through distance.) Naturally one would expect that a visual excitation (*i. e.*, one accurate enough to assist in orientation) would cease at the point where a clear image ceased to be formed on the retina. But the disappearance of a clear image on the retina does not mean a lack of visual excitation, according to Hachet-Souplet; for, as the bird gets further and further away, the clear image gives place to an "*imprecise*" visual impression, corresponding less to the perception of form and determined colors than to a sense of "*déjà vu familier.*" The impression becomes "mixed" in the sense that it bears elements of many different objects. He likens the view that the bird gets of a distant goal to our view of a distant forest. When one looks at a distant forest one does not see the leaves, and not even the trees separately. This author thinks that the "mixed impression" is serviceable at a much greater distance than is ordinarily supposed, and he states that refraction adds greatly to the distance at which it may function. He maintains that all of the calculations showing the heights to which birds must fly to see the côte have been exaggerated because they have not been properly corrected for refraction. Given the curve for refraction, it will be possible for the birds to obtain these

---

*Hachet-Souplet: VI. Cong. Int. de Psy., 1909, p. 663.

"mixed impressions" at all the distances from which they ordinarily home. It is well to note (1) that it is not during the forward journey that these "memories" are graven in the memory of the bird (they come from previous flights), and (2) that these memories which are able to be considered as effective are not memories of precise form, but of special impressions of *déjà vu*.

Hachet-Souplet gets around many of the facts by denying them. He says:

> One fact which appears out of harmony with the theory of orientation by view are the returns from 800 to 1,000 km. which pigeons have effected without training in a direction entirely unknown to them, but these facts are controverted for the most part and are always exaggerated.

Where the facts are incontestable he would explain them on the basis of chance. Most of the flights which are considered in our own paper are far beyond this limit set by Hachet-Souplet.*

Schneider's† conclusions are numerous, the one of chief interest being as follows:

> The assumption that the carrier pigeons possess an inborn sense of direction is an error; for if this assumption were true, then the young pigeons ought to find their way equally well. The investigations have shown, especially those at Könitz, that young pigeons, even at relatively small distances from their home, have the greatest difficulty in finding their way back when the vicinity is at all strange to them, and their home can not be directly seen.

He then concludes that the young birds utilize, in their early flights, the familiar groups of houses, mountains, etc., and that the distances to which a bird may be taken safely may be increased commensurately with the increase in the development of his "topographical memory." This author believes that the pigeon can develop not only "Errinerungsbilder" but even "Gedächtnisse." Schneider had had wide practical experience before reaching these conclusions.

Like the previously considered observers, Hodge‡ finds no necessity for assuming a sense of direction in the homing pigeon. His experiments were made largely upon young pigeons. When they were first released at the côte they circled about the côte, then flew from one distant point to another, and thereby (according to this author) established a system of *visual landmarks*. Young birds taken in an open cage half a mile away from the côte returned with few circling flights; but young birds removed in closed cages circle, make errors, and even fly for long distances in a wholly wrong direction. Training produces almost immediate results in good birds. Only after training do they take a straight line and behave as though they had a sense of direction.

When placed in an unknown neighborhood the bird begins upon a "line of search." "The logical curve of search is a peculiar spiral, the involute of a circle, the characteristic of which is that the convolutions are always the same distance apart. These distances will be, of course, twice the distance at which the object is visible."

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*According to Sébillot, quoted by Hachet-Souplet, when homing pigeons are released at the sea the altitude at which they fly increases proportionately to their distance from the land. At 146 km. the pigeons scarcely pass over the normal altitude of 150 to 300 meters; at 200 km., they had visibly mounted much higher; at 300 km., the altitude was found to be at least 600 meters. In the final test we lose the birds from view in the heights and not at the horizon.

†Schneider, G. H. Zeitsch. f. Psychol. u. Phy. d. Sinnnes., 1905, XL, pp. 252–279.

‡Popular Science Monthly, 44, p. 758.

In accordance with this theory Hodge finds as follows:

> Of a large number of birds sent away by rail for longer flights, not one made the return trip in less time than would have enabled him to fly on the involute of a circle from the place of liberation. This refers to "first flights." The best time made was 26 miles in 5 hours and 9 minutes. Three other birds liberated at the same time failed to return. Letting the distance to which a prominent landmark is visible be 3 miles, a fair estimate for pigeons with some training and over broken country, the least length of an involute of a circle which would bring a bird from a distance of 26 miles to within sight of the loft is 219 miles. In 5 hours it is not likely that the pigeon flew less than 250 miles.

Duchâtel[*] advances the highly speculative view that the retina of the bird is sensitive to infra-luminous rays, especially infra-red, the waves of which are supposed by him to follow the surface of the earth, and consequently are not interrupted by its sphericity. In answer to this speculation we are now in the position to state that the retina of the homing pigeon is no more sensitive to these rays than is the retina of the human being. It was to meet Duchâtel's supposition that we undertook the work on spectrum sensibility in birds, the result of which is shown on pages 87 to 104 inclusive.

EXPERIMENTS SHOWING IMPORTANCE OF VISUAL IMPULSES IN HOMING.

It is generally agreed that pigeons home with difficulty in cloudy weather. Rodenbach[†] released 6 good pigeons at 10 a. m., 30 km. from their côte. The sun was obscured by clouds. None of the birds returned the same day. Two returned the second day after the clouds had partly disappeared; two on the third; and two failed to return. Furthermore, Hachet-Souplet[‡] shows that they do not home at all at night. He released pigeons at different hours of the day as follows:

No. 1 at 8 a. m., returned at 8^h 25^m.
No. 2 at 10 a. m., returned at 10^h 20^m.
No. 3 at 12 m., returned at 12^h 20^m.
No. 4 at 4 p. m., returned at 4^h 30^m.
No. 5 at 8 p. m., returned at 4^h 15^m the following morning.
No. 6 at midnight, returned at 5^h 5^m the following morning.

From this Hachet-Souplet draws the conclusion that the birds are guided back to their nests by an "*attraction visuelle.*" He neglects to take into account the records we have upon birds which migrate at night.

Rodenbach also made a test on a blind pigeon. After recovery the pigeon was placed before the entrance to its côte. Guided by the voices of its companions it was able to enter the côte and to beat its way to the right or left. On the following day it executed this feat more easily. On the third day it was taken some distance from its côte. Again, guided by hearing, it joined its companions on the roof. With great difficulty and by making desperate efforts it was able at the end of 2 days to reënter the côte. Some days later the bird was released in an open field at a distance from its côte which a sound bird could cover in 10 minutes. The blind bird flew vertically upward without circling, then to the south in a direction opposite to its côte. The bird never returned. These results agree with those obtained by Hachet-Souplet upon good fliers which had become blind. These birds, when released within 4 leagues of their côte, flew away and did not return.

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[*] Ann. de psych. zool., I, 1901, p. 22; II, 1902, p. 48.
[†] Rodenbach. Zeitsch. f. Brieftaubenkunde, 1895, p. 134.
[‡] Hachet-Souplet. Annals de psych.-zool., II, pp. 33–60.

EVIDENCE AGAINST HACHET-SOUPLET'S THEORY BASED UPON MATHEMATICAL CONSIDERATIONS.

The evidence we offer below militates against any theory of return over long distances at sea based upon vision. It immediately discredits Hachet-Souplet's theory of "direct perception of the goal" (as applied to the terns).

The distance at which an object is visible at sea is expressed approximately by the formula $d = 1.317\sqrt{x \text{ in feet}}$, where d is the distance of the object in statute miles and x the height of the object above the earth's surface in feet. The altitude obtained by this formula is, for shorter distances, approximately that obtained by calculating the tangent to the arc of the distance and correcting for the mean refraction at the horizon (36′ 29″), but for great distances the value obtained is somewhat too great. However, for our problem this error is negligible.

TABLE 1.

Distance.	Height to which bird must fly to meet light-waves reflected from land lying just above sea-level.	Height to which bird must fly to meet light-waves reflected from top of lighthouse.	Least object visible, 30″ acuity.	Least object visible, 4′ acuity.
statute miles.	*feet.*	*feet.*	*feet.*	*feet.*
18	186	3.4	137.0	1,100
65	2,430	1,407	496.0	4,012
	miles.	*miles.*		*miles.*
105	1.2	0.9	792.0	1.2
191	4.0	3.3	1,415.0	2.2
269	8.0	7.0	2,059.0	3.1
300	9.8	8.8	2,270.0	3.4
400	17.4	16.1	3,062.0	4.6
500	27.3	25.6	3,801.0	5.8
582	36.9	35.0	4,435.0	6.8
			miles.	
700	53.5	51.1	1.0	8.1
800	69.9	67.2	1.2	9.3
900	88.4	85.4	1.3	10.4
1,000	109.2	105.8	1.5	11.6
1,100	132.1	128.4	1.6	12.8

The second column of table 1 gives the height at which a bird must fly in order that its eye may meet with rays reflected from an object at sea-level at the distance indicated in the first column, provided that the bird is stimulated only by light waves ranging from 400 $\mu\mu$ to 700 $\mu\mu$ in length. The lighthouse upon Loggerhead Key is 151 feet in height. The third column of the table gives the height at which a bird must fly in order to see the upper 10 feet of the light tower at the distances given. Even upon the assumption that the birds have absolute visual acuity, it is evident that they can not fly high enough to be guided by light reflected from the goal for more than a small fraction of the distance through which they find their way back. But the limitations of acuity are probably even greater than those imposed by the curvature of the earth. For man two points of light are not distinguishable unless they are separated by at least 30″ of arc. Hence for a coast-line to be recognizable to man it must present inequalities of elevation which amounts to at least 30″ and these must be relatively abrupt.

The fourth column of table 1 gives the least observable inequality in the coast-line for the distances in column 1 for man.

The only data upon acuity in birds has been presented by Johnson* on the chick and places its acuity at about 4′. The fifth column in the table gives the smallest inequality in the coast line which can stimulate such an eye at the distances indicated in the first column. The most irregular mountains in the region of the Gulf of Mexico, where our observations were made, the Sierra Madre, would have, at a distance of 300 miles, the same stimulating value for the eye of this bird as a fine straight line seen a few feet away, the irregularities being lost in the imperfections of its dioptric mechanism. If the visual acuity of the homing bird is no greater than that of the chick, or even of man, the possibility of its reaction even to an "imprecise" visual impression seems precluded for distances of more than 100 miles.

A THEORY BASED UPON CUTANEOUS SENSIBILITY.

Cyon,† although he has contributed largely to our knowledge of the structure and function of the labyrinth, does not wish to be confused with those writers who attribute to them any special function in distant orientation. Naturally they are brought into play in the flight of the bird, but only as a reflex mechanism involved in the maintenance of equilibration.

In 1897 Cyon first announced his own theory. The theory advanced posited a *Spürsinn*, which has its location in the nose. This sense may be wholly independent and separate from the ordinary olfactory sense. In support of his theory Cyon refers to the well-known fact that the hunting-dog can at great distances find a person to whom he is attached. Why should not the homing sense be bound up in other animals with this sense? The fact that the sense of smell is so little developed in birds can mean nothing but that they are not sensitive to odors which affect the human being. This fact does not militate against the view that the organ of homing may have its seat in the same organ, without being identical with the olfactory organs. Many people from their youth are lacking in the sense of smell; they show a remarkable inability to orient themselves, not only in cities with which they are most familiar, but also in large buildings, especially if the latter are laid out symmetrically. They require time to orient themselves in a new building. Cyon suggests also that the work of Bethe on ants and bees seems to speak for a division in the olfactory sense.

Cyon's preliminary experiments showed that the birds were insensitive to ordinary smell substances. The birds showed no reactions when oil of cajuput and asafœtida were offered. On the other hand, they were found to be so very sensitive to ammonia that it may be used to test the anæsthetizing effect of cocaine. Fanciers sometimes hold that pigeons react to the nest by reason of smell. To see if this was well founded, Cyon blinded a brooding pigeon by closing the eyes with cotton soaked in collodion. The experiments were carried out in a house the third story of which contained a côte. The bird remained immovable. She only flew when tossed up in the air. In spite of the open door, she made no effort to return to her nest. Even in the vestibule she made no attempt. She did not return to the nest if placed just in front of it, but remained on the spot. This test shows only that the ordinary olfactory sense is not acute in the pigeon.

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*Journ. Animal Behavior, 1914, p. 340.

†Cyon, E. von: Ohrlabyrinth, Raumsinn und Orientirung, Pflüger's Archiv, LXXIX.

On the basis of an experiment to be described, he advanced the view that *the direction and temperature of the wind act upon the olfactory mucous membrane.* As we understand him, his theory is based, on its sensory side, upon the functioning of the tactile nerves (largely Vth) in the nasal cavity.

Cyon's experimental data in support of this theory are exceedingly limited. He selected 3 young homing pigeons of equal age and ability, which had been trained to return from distances of 4 to 500 km. (direction not stated). Pigeon A was used as a norm. Pigeon B had the anterior nares closed with a cocaine-saturated plug, the whole coated with collodion. In the same manner the auditory meatus of pigeon C was closed. The 3 birds were carried at 7^h 30^m a. m. from Spa in a railway carriage to the station at Huy, which by rail was 60 to 70 km., and in an air-line, 50 to 55 km. from Spa. Huy was chosen because it lay in a valley and was separated from Spa by a mountain. The weather was clear and fine. Pigeon C did not stand the trip very well and ate apathetically the day before release. They were released in the following order: A, at 10^h 13^m a. m.; B, at 10^h 19^m a. m.; C, at 10^h 26^m a. m. There was some difference in the orienting flight. The norm, A, arose perpendicularly and began to make the characteristic circular flights. It then took suddenly the direction of northwest, following the line of the railway. B ascended fully as rapidly, but not perpendicularly, veering towards the east. Finally it took the direction south. C was released 7 minutes later and arose with slower speed; its circles were smaller; oftentimes, in place of going higher, it descended. It took the direction east. Pigeon C (auditory meatus closed) was the first to reach home, at 11^h 35^m. It required, therefore, 1 hour and 9 minutes for the trip. The normal pigeon appeared at 12, requiring 1 hour and 47 minutes. It probably chose the railway back, going through Lüttich and Peppinster, while C probably chose the air-line. Pigeon B (nasal passages closed) appeared 4 days later, September 6, between 4 and 6 p. m. This bird required 78 to 80 hours for the trip. It was found that the nasal passage was completely clear, both of the cotton and collodion.

Cyon does not believe that this belated return was accidental, nor that the pigeon was held in durance, because a large price was offered for a report of it. He feels that the bird wandered more or less aimlessly until it could free its nose of the plugs, after which it sought its way home. Cyon's position may be summarized as follows: (1) Orientation, in the last analysis, depends not upon purely instinctive and reflex processes, but upon intelligent adjustment (habits based largely on cutaneous sense). (2) Orientation is attained with the help of two senses: " . . . des Gesichtsinnes und eines speciellen Spürsinnes, der in der Schleimhaut der Nase (und vielleicht der Stirnhöle) seinen Sitz hat. Letzteren Sinn kann vom Geruchsinn unabhängig sein. Er wird vorzugsweise durch die Qualitäten der Winde (Richtung, Intensität, Temperatur, . . .) in Thätigkeit versetzt." (3) The vestibular portion of the ear functions only as an equilibratory mechanism.

EVIDENCE AGAINST CYON'S "SPÜRSINN THEORIE."

On June 16, 1910, a test was made at Tortugas of Cyon's hypothesis which has just been considered. Three noddy terns were captured on the night of June 15. On the morning of June 16 the anterior nares were first sponged out with alcohol to remove all secretion, and then filled with warm wax, packed in. The whole was then coated with asphaltum. The feet of the birds were tied and they were put back in the cages until the asphaltum had had a chance to dry. The feet were left tied also during the transit of the birds, since this prevented them from scratching at the wax and gave them a chance to become habituated to it. Two of the birds, in charge of Mr. Rufus Mills, were sent to Key West and the third (the control) was sent to Loggerhead, 3 miles away. The Key West birds were released at 2 p. m. The nests were observed that night, but apparently they did not return. At daybreak the next day the two birds were both found upon their nests. Since the nest mate was just leaving one of these birds, I am inclined to think that at least one got back on the same afternoon in which it was liberated. The control bird was released at Loggerhead at 7 p. m., in plain sight of Bird Key, with head directed towards Bird Key. Drs. Mayer and Treadwell were both present. This bird flew to the water and bathed, then flew slightly eastward in a straight line to Bird Key; it was on the nest when the experimenter reached there, 30 minutes later. It was found that the plugs in the anterior nares were present in all three birds. The asphaltum was not even scratched and had hardened completely. The birds had resumed their nesting activities. This test (so far as the terns are concerned) seems to be absolutely conclusive against Cyon's hypothesis.

REFLEX THEORIES.

REFLEX THEORIES BASED ON THE FUNCTIONING OF SEMICIRCULAR CANALS.

Reynaud,* although having at his command the best facilities for making scientific observations, has contributed little on the factual side to the study of homing. For some years he had charge of the movable côtes of the French army, and later of the carrier-pigeon post of "La Compagnie Transatlantique." His theoretical views have been crystallized into a "loi du contrepied." This law merely states that the pigeon returns by the route over which it was carried, retracing, on return, all of the windings of the forward trip. He tries to get some factual support for this law by keeping a record of the finding of lost birds. The birds at times disappear and are usually found, according to him, at some point on the route over which they have been carried. His records, however, are extremely sporadic and are of no scientific value. He assumes, furthermore, that there is proof for his theory in the great migration routes of birds and in those of fishes. He maintains that both the forward and the return migration routes are the same in every case, and that certain species of both birds and fishes have practically been exterminated by sportsmen because of their adherence to these routes. That such is not often the case has been quite clearly shown by Cooke, who proves very plainly that in many cases Northern and Southern migrations do not take place along the same route. The most notable example of this is to be found in the plover (see p. 29).

Like a good many others, Reynaud places the mechanism of return in the semicircular canals. The stimuli to it, although not clearly defined by him, are practically the same as those of Bonnier. The twists and turns which the bird receives as it passes over the forward route are stored up in some way so that they become effective as stimulators when the bird returns (see Bonnier's attitude theory).

A crucial test of Reynaud's theory could easily have been devised by him by taking the bird along an extremely circuitous route and then releasing him, *e. g.*, not more than 300 miles from his home. If the bird returned at the end of 5 to 6 hours, we may be sure that it returned by the direct route. If, on the other hand, several days were consumed, we might have some grounds for supposing that the longer route was chosen. He maintains that he has made such tests, but no satisfactory publication of them has ever been made. (See reference to other articles by Reynaud, in Claparède's bibliography.)

Bonnier† advances a theory (no experiments given) which may be classed, despite its appeal to memory, as a reflex theory. It was put forth after the contrepied theory of Reynaud and does not differ from it except in attempting to account for direct returns (that is, for known cases where the bird does not retrace the various stages of the forward journey, but on the return takes a direct route). According to Bonnier there are two general methods of orientation. One is able to orient oneself on the moment of arrival or at the instant of departure. In order to orient in advance, or at the moment of release, landmarks (*repères*) of one kind or another are necessary. But in many cases the conditions are made such that landmarks are not at hand. Hence, Bonnier believes that orientation is always obtained by reference to the *point*

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*Bird Lore, 2, pp. 101–108; *ibid.*, pp. 141–147.

†Bonnier, P.: L'Orientation, Scientia, No. 9, 1900.

of departure. The point of departure is a landmark (*repère*) forcibly known to us, since we go directly from it. By remembering all of our displacements since our departure we remain, after a fashion, in continual contact with this point. Whenever we are distant from it we strive, without keeping detailed accounts of these displacements (even unconsciously), to maintain at every moment the notion of its direction with reference to the course of our displacements. The consciousness of the point of departure is a fundamental base and suffices for all our operations. The idea of its orientation, that is to say, of its displacement with reference to us, increases in clearness just in proportion as we feel that we are displaced with reference to it. This idea is furnished by the operation of the sense of total "aptitude" (*aptitudes totales*), the ampullar sense of our 3 labyrinthian canals (". . . *le sens ampullaire de nos trois canaux labyrinthiques*"). The memory which supplies this notion fixes it and preserves it just in the proportion that memory itself develops. This memory is but an aptitude, not more astonishing than many others, and it is natural that this aptitude should have acquired, by hereditary accumulations, an extraordinary power in the species in which the exercise of this instinct is a condition of survival and an important factor in evolution.

We have given above as faithful a presentation as we can gather of Bonnier's position. We have attempted where possible to give a free translation of his writing. So far as he advances the hypothesis of orientation by appeal to displacement, we presume Reynaud would agree with him. Bonnier then advances the idea that individual birds differ in their capacity to orient, as follows:

> The homing pigeon, transported in a basket, holds fast to the memory of the direction of the point of departure (in spite of the various successive passive displacements). Arrived at the point of release, he has not for a moment lost the precise notion of the component displacements or of the total displacement. This notion, condensed by memory, is like the thread of Ariane which he attached to his point of departure. If he is not quite sure of himself he retraces stage by stage the road which bore him to the distant point—but if he is expert in distant orientation, he holds directly to the thread in place of following its twists and turns. He relies upon direct orientation, on the notion of the point of departure, an idea which he guards in proportion to his displacement, relying among all these detours only upon this constant idea of the sense of return, or orientation from the point of departure [*i.e.*, as we understand Bonnier, the bird resorts to a kind of triangulation process]. It is to be presumed that expert birds in distant orientation have a more highly organized hereditary memory.

Bonnier's aptitude or displacement theory, if such we may call it, must be looked upon as a suggestion, and one which is extremely vague at that.

REFLEX THEORIES ASSUMING MAGNETIC SENSIBILITY.

Viguier,* basing his views upon the "absurdity" of supposing that a bird can fly high enough to perceive its côte when at long distances at sea, and that migrating fish can run their course through vision or smell, maintains that the physical force which enables animals to direct their course must be everywhere present, "in the heights of the atmosphere as well as in the depths of the sea." This force is terrestrial magnetism. To the objection (already raised by Darwin) that a compass without a chart avails but little, Viguier replies:

> Is this objection insurmountable? I think not. The compass gives to our mariners a simple direction. They need to know the angle that this direction makes with their route

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*Viguier, C., Revue Philosophique, 14, p. 11.

> in order to direct themselves. It is the chart which serves this purpose; and if one conceives of animals endowed with a sense which permits them to recognize only the direction of magnetic north, these animals would have a constant notion of north, but would not be capable of returning to their point of departure unless they had maintained an exact memory of the length of the lines traversed in this or in that direction. The mariner, navigating by dead reckoning, has to write down the length as well as the direction of all his rhumb lines. Such a view demands at least a constant perception and a prodigious memory and does not correspond at all to the simplicity of the notion of which I spoke above. But terrestrial magnetism furnishes other indications. If we suppose that an animal is capable of perceiving influences which actuate the needle of the compass of inclination, and that the position of this animal remains always the same with respect to the vertical of the place, he will be able to recognize the differences in intensity which cause the variations in the angle which we measure with the aid of this compass, an angle which varies, as we know, from 0 degrees at the magnetic pole to 90 degrées at the magnetic equator. He would be able, then, to recognize the direction where this angle varies most quickly (magnetic meridian or isogonic line), and where it remains constant (magnetic parallel or isoclinic line). Finally, there are other data which we may gather from the use of our instruments, and which one can suppose perceptible through an appropriate organ. We have in mind variations in magnetic intensity. If one disturbs the position of equilibrium of the needle of the compass of declination, the needle comes back, by a series of oscillations, which show a variable force according to the place. By joining all the points where this force is equal we can trace on our maps a series of lines (isodynamic) which can be confused neither with isogonic nor with isoclinic lines (although they show a development somewhat like that of the latter). One can then admit that a line can be determined for an animal, endowed with the magnetic sense as complete as we are assuming it to be, by the value of the magnetic actions in inclination and declination, just as fairly as it would be determined for us by the intersection of given magnetic lines. These magnetic conditions once known, the animal will be capable always of going directly to this point. Carry it to considerable distances, cause it to describe complicated circles, anæsthetize it even during transport, it will be able always to come back to its point of departure. This sense is supposed to give the animal general direction. It will suffice to bring it into a neighborhood where the five senses can be employed.

He supposes that the magnetic currents act in such a way as to release reflexes. The tissue affected is specified as follows:

> Assume, then, that terrestrial magnetism induces true currents in the endolymph of the canals, the intensity of which varies with the position of these canals with respect to the directions of the needles of inclination and declination, and with the intensity of the magnetic phenomena.

Thauziès,* likewise, as is well known, believes that the magnetic theory is the only one which will account for the various facts of homing. In his description of this theory he makes the following statement:

> The pigeon possesses a *sensibilité magnétique* which permits it to receive impressions quite special and even somewhat mysterious—terrestrial magnetic currents, lines of force, etc.—the influence of which combined with the work of the other senses puts the animal on the true route and enables it to maintain it.

Thauziès favors this theory because it is "logical" in appearance and because it brings into play the "mental activity" of the bird. Thauziès has had an immense amount of practical experience.† For 23 years he has made

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*Thauziès, A.: L'Orientation lointaine, VI. *Cong. Int. de Psy.*, 1909, p. 263.

†He states that the distance from which a pigeon can return is rarely greater than 500 km. As a matter of fact, most of his flights lie well within this distance. He tells us further that, so far as he knows, this faculty of orientation is not lost through age. At the age of 20 years a pigeon is no longer fit for service. The quickness of flight attains to 110 to 120 km. to the hour, but it varies according to the direction which the pigeon has to follow. These statements were made in reply to questions asked at the time the paper from which we quote the above was read.

observations at his côte in Perigueux. He gives little material which is serviceable in solving the problem of homing. One statement he makes which is useful is that the birds rarely fly higher than 300 meters; the average height is 150 meters. If a mountain range causes them to fly high in passing they immediately fly down again and stay near the surface of the earth. The only really positive evidence which Thauziès advances in support of the theory comes from the parallel records which he has kept of disturbances in flight and of disturbances in terrestrial magnetism. We summarize the facts from two cases:

> On August 18, 1907, the Société Colombophile, of which I am a member (L'Hirondelle de Perigueux), released at Orleans (320 km.) at 6^h 30^m a. m., on a bright calm day with slow south wind, 99 young pigeons which, up to that time, had given perfect satisfaction." ". . . this journey, which we would have thought extremely slow if completed before mid-day, was not completed by any bird before 2^h 43^m. Only 11 subjects came back before night, the rest the following norning. It was so abnormal that we made inquiries of others. We learned that most of the societies in these regions who had pigeons *en route* had been as surprised as we ourselves were by the tardy home-coming of their birds. The year preceding, on July 22, we had been victims of a yet more singular misadventure. Our young pigeons released at Angoulême (65 km.) at 10 o'clock under an admirable sky, limpid and without wind, required more than 3 hours to make the journey, which should demand scarcely an hour. Many birds were even later than this and many were lost altogether. On taking up the matter with the Astronomical Department we found that on July 22, 1906, and on August 18, 1907, there were severe electrical storms.

Thauziès's observations are incomplete because of the fact that there may have been many just as violent electrical storms which produced no retardation in the flight of the birds. Until the test has been worked both ways, one can not draw any conclusions, and even if an electrical disturbance did produce a retardation of flight, this would not necessarily imply that the birds were using terrestrial magnetism as a means of orientation. There are possibly other phenomena connected with electrical disturbances which may have produced the effect. The correlation, if it could be made, would be exceedingly interesting.*

EXPERIMENTAL EVIDENCE AGAINST THE REFLEX THEORIES.

Exner† has made the most careful experiments to be found in the literature on the conditions which affect flight. If his results could be confirmed under slightly better conditions they would certainly discredit both Reynaud's theory and certain of the theories based on magnetic sensibility. He tried the experiment of stimulating the birds with an electrical current during the forward journey; anæsthetizing the bird, rotating it, etc. His experiments were carried out near Vienna. Several experiments of the following kind were made: birds were carried in a box arranged for the giving of electrical stimulation; electrodes were placed upon the head in such a way that a current could be made to pass through the semicircular canals, etc.

> Quer durch den Kopf geleitet, bewirkt ein galvanischer Strom bekanntlich bei Mensch und Thier Schwindelgefühle, das heisst die Empfindung einer Drehung oder Neigung, deren

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*The U. S. Weather Bureau at Washington has offered to coöperate with us in attempting such correlations. It may be possible to warn an observer in advance of the possible approach of an electrical storm (approach of sun-spots, etc.). It would seem feasible, with such a warning, to ship the birds several hundred miles and then release them and note the returns.

†Exner, Sigmund: Negative Versuchsergebnisse über das Orientirungsvermögen der Brieftauben, Stizungsberichte der Kaiserlichen Akademie der Wissenschaften (Wien), p. 318.

> Sinn von der Strommesrichtung abhängig ist. Es ist das der sogenannte galvanische Schwindel, auf den hier einzugehen nicht der Ort ist. Bei der Taube verräth er sich durch Neigungen des Kopfes, Augenbewegungen u. s. w. Ich suchte also während der Hinfahrt das Thier durch diese Drehempfindungen über die thatsächlichen Wendungen und Drehungen zu täuschen. Wenn der Vestibularapparat das Thier während der Hinreise orientirte, so müsste durch das Hinzutreten des galvanischen Schwindels diese Orientirung vernichtet werden, oder doch zu einer Orientirungstäuschung führen.

The birds were continuously stimulated all through the forward journey. Upon reaching their destination they were freed from the apparatus and released. The first release was made 54 km. from Vienna. They were all released on April 16, with the following results: (1) the adult control bird (armed with the same apparatus during the forward journey, but not electrically stimulated) was released at 11^{h} 11^{m}, reaching Vienna in the early morning of April 18; (2) the young control bird, released at 11^{h} 16^{m}, did not return; (3) adult bird electrically stimulated, released 11^{h} 18^{m}, reached Vienna on the same day at 1^{h} 50^{m}; (4) young bird electrically stimulated, released at 11^{h} 32^{m}, did not return.

Many other experiments of this type were made, with essentially the same results. As many birds electrically stimulated returned as normals. Exner next completely anæsthetized with ether several adult and young birds and kept them so during the whole of the forward journey. On reaching their destination the birds were restored and allowed a certain length of time for recovery, and were then released. In the first experiment they were released 43 km. from Vienna. The results were: (1) normal animal, released at 6^{h} a. m., did not return; (2) anæsthetized animal, released at 6^{h} 20^{m}, did not return; (3) anæsthetized animal, released at 6^{h} 49^{m}, returned at 11^{h}; (4) normal animal, released 10^{h} 21^{m}, returned at 12^{h}; (5) young normal animal, released at 10^{h} 26^{m}, did not return; (6) old anæsthetized animal, released at 10^{h} 30^{m}, returned at 12^{h}; (7) young anæsthetized animal, released at 10^{h} 35^{m}, did not return.

From these experiments of Exner, it is evident that he worked with very poor material, that is, with birds which were poor flyers. Nevertheless, it seems clear from his experiments that electrical stimulation, anæsthetization, etc., during the forward journey have a negative result upon the return of the birds.

INFORMATION ON HOMING PIGEONS GATHERED FROM PRACTICAL FLIERS.

We give below a letter written us by a well-known practical flier in this country, Mr. A. E. Wiedering, for many years race secretary of the Milwaukee district of National Federated Homing Pigeon Fanciers. Mr. Wiedering's letter, while in part touching upon theoretical questions, contains also a large amount of material dealing with the training of the birds.

I was race secretary for several years and took a keen interest in the sport. In the spring of the year we would begin to train the birds over short distances, beginning with 3 or 4 miles, and then 9, 18, 33, 45, 66, and from then on 100, 200, 300, 400, 500, 600, 700, 800, and 1,000 miles. Speaking about training the birds over short distances, we come to a point that has always been under considerable argument with the fanciers. Some claimed short-distance training of great value and others considered it as a waste of time and labor and as entirely unnecessary. I agreed to a certain extent with the latter, as I was of a firm opinion that little is gained by flying the birds over short distances, that their homing instinct, since it is so called, is not developed or improved by it. The only advantage in short distance flying that I could see was that the birds got good opportunities to get used to the shipping baskets and as they felt more at home in them would more readily begin to feed and drink in them, and in that way remain in better condition for their home flights.

After several years of participation in the fancy, I advanced the argument that it was a harder task for a bird to get its bearings towards home from a short distance than from a greater distance. Careful observations of the birds' activities brought me to this belief.

The birds, I believe, home to the locality that they have been used to and not exactly to their loft. I mean that this drawing towards their home location ceases when they get within this locality, and that after that they find their loft through memory of sight by familiar landmarks, etc. I imagine a circle around their home of an imaginary distance of say 5 or 6 miles, and that their homing instinct is not brought into action until they are beyond this locality circle, and if liberated within this circle they have to depend upon their sight memory in order to find their home. I have liberated birds that have had years of experience within 3 and 4 miles of their loft and have seen these birds fly around and around for hours completely at a loss, it seemed, as to their location, and have seen them fly in the opposite direction of their home. Some of these birds had the best of reasons for returning home immediately, such as a hen hatching her egg, or a cock desiring the hen, in which cases they are more eager than usual to return home.

Then again I have been informed by liberators at long distances that the birds had taken the right direction after making a few circles; the best start was made from 1,000 miles, our greatest distance flown, the birds taking the right direction without circling, but starting for home at once. From distances of 100 miles and less the same birds had circled for over 30 minutes and did so repeatedly. From such facts I came to the conclusion that it is easier for a bird to get his bearings from a long distance than from a short one; that this unknown feeling or instinct, or sixth sense, was more intense at a greater distance; and if the bird was liberated in its own locality it did not seem to be in force.

Little, if anything, can be learned of this homing sense by flying these birds; you ship them to a liberator; he liberates them, giving you conditions at the start; you see the birds returning home and know what your local conditions are, but do not know what kind of storms or air-currents the birds have to pass through, and you may have very good results from a flight on one day and from the same distance on another day may have very poor results, although the weather conditions at start and finish may be the same.

I used to stamp my address on flight feathers of the birds and used to hear from them, through parties who would catch them in their own lofts or pick them up dead. In most cases the birds would be found dead without any apparent cause. I believe that they would die from exhaustion.

The speed of a homing pigeon with hardly any winds would average about 1,400 yards per minute for about 100 miles. We have had the birds make it in an average of over 1,900 yards per minute with a strong favorable wind, and 600 yards with contrary winds.

With very favorable weather conditions we have had birds arrive home at 3 p. m. when liberated at $4^h\ 30^m$ a. m. from 500 miles, in apparently fresh condition. It may seem strange, if a bird can make 500 miles in one day why it should not make 1,000 miles in much less than 9 days, but it is supposed that the bird, after his best effort the first day, is exhausted and would look for food, and on account of poor condition, it takes several days before he can resume his journey. I had a bird return home after an absence of 5 years. One year I lost a bird from Walnut Ridge, Arkansas, 500 miles. The next year he happened to come home the very day we were again shipping birds to the same point. I was not very pleased with his performance the year previous and his absence for one year, and therefore shipped him again, feeling that he would surely not be able to return after his long absence and being in very poor condition. You can imagine my surprise when this same fellow was the first bird to reach home, making the distance within 12 hours.

Hobo, the bird that made the world's record from 1,000 miles, came to me when a young bird, quite sick; where he came from I did not know—he just walked into my loft, and being a good-looking bird I allowed him to remain and nursed him to health. He proved to be the most consistent performer I ever owned.

We give below a description of the training of the bird *Hobo*, together with a statement of the flight from Houston to Milwaukee. This note is of interest in view of the fact that it shows the training stages which are usually given a bird before long flights are expected of it:

A week ago last Wednesday [July 24, 1901] a number of birds owned by members of the Milwaukee district of National Federated Homing Pigeon Fanciers, were liberated at Houston, Texas, an air-line distance of 1,000 miles. Up to to-day two birds have arrived, the first to come home being the bird *Hobo*, owned by A. E. Wiedering, which arrived Saturday, and the second being from the loft of C. G. Loeber, *Little Hen*, which arrived yesterday, making the trip in 14 days 1 hour and 19 minutes. They are the first two Milwaukee birds ever to cover the distance, and the winner, *Hobo*, did it within but a few hours of the world's record. Several of the descendants of *Hobo* are flying in the service of *The Journal*. *Hobo* is a strongly built blue-checked cock and is now in his prime, being only 4 years old. He will not be flown again, as his owner thinks that he has done his duty. He has always been a reliable homer, but has hardly ever shown any speed in distances less than 600 miles. In 1899 he flew one race from Shabbona, Ill., at a rate of 50 miles an hour. In 1900 he won fourth place in a race from Little Rock, Ark., air line, 617 miles; 33 birds competing. He arrived at $5^h\ 30^m$ a. m. on the third day after liberation. This year he won second place from the same distance, also making it on the third day; 47 birds competing, but only two making it in the time limit for that distance, which is 3 days. After a week's rest he was shipped with 25 others to Houston, Texas, air-line distance, 1,000 miles. After being in the shipping basket 17 days, the 26 birds were liberated on July 24 at noon, all the birds taking their course immediately. *Hobo* arrived August 3, at $8^h\ 15^m$ a. m., taking 9 days 20 hours and 15 minutes to cover the distance.

Following is his complete record:

1898.
9 miles.
18 miles.
33 miles.
45 miles.
66 miles.
100 miles, Shabbona, Ill., to Milwaukee.
200 miles, Delavan, Ill., to Milwaukee.
400 miles, Ironton, Mo., to Milwaukee.

1899.
33 miles.
66 miles.
100 miles, Shabboth, Ill., to Milwaukee.
200 miles, Delavan, Ill., to Milwaukee.
300 miles, Brighton, Ill., to Milwaukee.
400 miles, Ironton, Mo., to Milwaukee.

1900.
33 miles.
45 miles.
66 miles.
100 miles.
200 miles.
400 miles.
617 miles, Little Rock, Ark., to Milwaukee.

1901.
18 miles.
45 miles.
100 miles.
200 miles.
300 miles.
400 miles.
617 miles.
1,000 miles, Houston, Texas, to Milwaukee.

Little Hen is 5 years old and has been in races for the last 4 years, and, although she has never made any phenomenal time, she has always been a reliable homer. This year she homed from a 500-mile station twice, and the amount of experience she has had on the road evidently stood her in good stead in this race, as the passage through the drought-stricken country was a severe one.

Since 1901 *Hobo's* record has been beaten many times. Many of the birds holding or having held world's records have belonged to lofts in Fort Wayne, Indiana. The fanciers in this city have succeeded in breeding a strain which is unrivaled in the history of homing. It would be interesting to determine whether the location with respect to winds, etc., has anything to do with the records these birds have made. The difference of course may lie wholly in the strain of bird which has been obtained. We give below the letter of Mr. O. W. Anderson, of that city. It concerns the record of the present world's champion, *Bullet D-1872.*

> This bird was hatched March 20, 1909, and when about 4½ months old began training, flying the training stations of 2, 5, 8, 15, 25, 40, and 75 miles and the young bird races of 100 and 200 miles; this bird being my first one in the 200-mile race. In 1910, as a yearling, she flew the training stations from 2 to 75 miles and on four successive Sundays flew the 200, 300, 400, and 500 mile races, arriving from the 500-mile race on second morning and the first three races the same day, being my first bird in all these races.
>
> In 1911 she flew training stations mentioned before; the 200, 300, and 500 mile races, arriving the same day in 200-mile race and the second day in 300 and 500 mile races, the weather conditions being unfavorable in these last two races.
>
> In 1912 she flew the training stations and 200, 300, and 500 mile races, arriving the same day from 200 and 300 mile races and fourth day from 500-mile race, but weather was extremely bad for this last race.
>
> In 1913 she flew the training stations and was first bird to my loft from 200-mile race, arriving on third day at 6 a. m., the weather conditions being very unfavorable on account of a very severe hail storm. She was also my first bird from 500-mile race, being liberated at $4^h\ 30^m$ a. m. at Springfield, Missouri, and homed at $3^h\ 26^m$ p. m. same day. Three weeks later sent her to Abilene, Texas, 1,010 miles (air-line measure) from here, birds being liberated at $4^h\ 30^m$ a. m. on July 11, 1913, and this one homed at 4 p. m. on July 12; flying time, 1 day 11 hours 30 minutes and 6 seconds. Needless to say, the weather conditions were ideal, a strong wind assisting the bird materially. In this same race a bird belonging to Dr. John Schilling of this city homed at $11^h\ 30^m$ a. m. the following morning (July 13) and a third bird was received by Mr. F. Nahrwald of this city a half hour later. The birds in this race were liberated by express agent at Abilene, Texas, as per telegram sent Racing Club here on same date, and liberating report bearing names of witnesses on file at office of club here.
>
> All the above races were in the Old Fort Homing Club of this city and were flown under rules of American Racing Pigeon Union. The best previous record for 1,000 miles was made by a pigeon belonging to Mr. H. Beech of this city in 1912, the time being 2 days 9 hours and some odd minutes, and this record lowered the time made by a bird belonging to Mr. L. Gebfert, of this city, in 1910, this time being 3 days 11 hours and some odd minutes.
>
> Have not entered my pigeon in any subsequent race, but am saving it for its record's sake, as there is of course a certain risk of loss of birds in any race.

From these startling records it must not be supposed that very many birds, flying from an average loft, return from 1,000 miles unless they have been previously trained over intermediate distances very completely. A few years ago over 100 homers belonging in Baltimore were released at Key West, Florida. Not one ever returned. All had been trained at least 500 to 700 miles from Baltimore in the direction of Key West.

THE RECORD OF A TYPICAL FLIGHT.

Thauziès* gives the record in detail of homing pigeons released by him at Geneva when the Sixth International Congress for Psychology was in session. The birds belonged to three cities, Versailles, Guéret, and Gannat; none of them had flown from Geneva previously. The Versailles birds had been trained toward Brest, the Guéret birds towards Amsterdam. Four of the birds from Gannat had already been trained from Macon to Gannat. He says nothing of the training of the other four Gannat birds.

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*Thauziès, A.: Expérience d'orientation lointaine, Archives de psychologie, IX, 1910, p. 66.

Versailles birds: 24 birds were released in Geneva at 7^h 10^m August 6; 2 returned the same day at approximately 5^h 45^m p. m.; 9 returned August 7 at different hours; by August 10 all had returned.

Guéret birds: 34 birds were released in Geneva at 7^h 15^m on the morning of August 6; 2 returned the same day a little after noon. The rest returned on the following morning.

Gannat birds: 8 pigeons were released in Geneva at 7^h 20^m a. m., August 6. None returned the first day; 3 returned on the morning of August 7; 1 on the 8th; 1 on the 9th; 1 on the 11th, and 1 on the 12th. On August 17, 1 bird was still out.

We give this record of pigeons in full because it brings out one point very clearly, viz., that even in short flights all of the birds do not return promptly. Those we read of in the homing-pigeon records are usually of the first bird in the loft to return and it is rare that all of the birds from any given loft return on the first day, even when the distances are short. The above distances were all very much less than the longer flights made from Bird Key. The distance from Geneva to Versailles is 280 miles, to Guéret 220 miles, and to Gannat 150 miles.

DATA ON THE SPEED OF THE HOMING PIGEON.

The following record was furnished us by Mr. Wiedering. It relates to average speed in a 200-mile contest.

161 birds were shipped on Saturday to Delavan, Ill., being a little over 200 miles on an air-line. The birds were liberated on Sunday at 7^h 10^m a. m. by W. M. Cornett, agent of the Chicago & Alton Railroad Company, who reported weather fair and wind from the southeast. At home the weather was very cloudy and the wind from the south, changing to east about an hour before the arrival of the first bird. According to reports local showers prevailed along the greater portion of the course and the speed made is very satisfactory, under the conditions. The first bird timed at the several lofts and the speed per minute attained by each is as follows:

Alex. E. Wiedering, 1,135.30 yards.
H. J. Baumgaertner, 1,134.61 yards.
Aug. Bergenthal, 1,134.59 yards.
John Radke, 1,127.99 yards.
William R. Knell, 1,115.71 yards.
Edw. J. Phipps, 1,081.48 yards.
Val. Burkard, sr., 1,067.99 yards.
Peter J. Ries, 1,003.19 yards.

When the distance is shorter the average speed, with other conditions equal, usually rises. From the same source we have obtained a record for a 100-mile flight:

The Milwaukee district of the National Federation of American Homing Pigeon Fanciers conducted its 100-mile race from Shabbona, Ill., on Tuesday, May 31. 161 birds were shipped by Adams Express on Saturday of last week. The weather being unfavorable on Sunday and also on Monday, liberation did not take place until the date above mentioned.

A. J. Harton, agent of the Chicago, Burlington & Quincy Railway, acted as liberator, and reported that the birds were liberated at 6^h 30^m a. m., with clear weather and southeast wind. At home the weather was also clear, with wind changing from southeast to southwest.

A bird from the loft of H. J. Baumgaertner was the winner of the race, and covered the distance of 101.27 miles in 2 hours and 43 seconds, being at the rate of 50.30 miles an hour.

The first bird timed at each of the respective lofts, with the average speed per minute, is as follows:

H. J. Baumgaertner, 1,475.60 yards.
William R. Knell, 1,471.29 yards
A. E Wiedering, 1,452.89 yards.
Aug. Bergenthal, 1,411.29 yards.
Edw. J. Phipps, 1,395.07 yards
P. J. Ries, 1,373.69 yards.
Val. Burkard, sr., 1,349.08 yards.

The above agrees closely with Ziegler's[*] account of the flights of German birds. According to this author the direction and velocity of the wind greatly influence the flight of the birds. In flights from great distances (100 to 600 km.) the average speed of the best birds with no wind is 1,100 to 1,150 meters per minute. In a favorable wind the speed rises to 1,300 to 1,600 meters, and occasionally to 1,600 to 1,950 meters. In unfavorable winds the speed of the best birds varies from 500 to 800 meters, according to the strength of the wind. The pigeons never fly to great heights—never over 1,000 to 2,000 meters and usually much lower.

THE PROBLEM OF HOMING IN BIRD MIGRATION.

In this paper, as has been stated, we shall not discuss the general features of bird migration. Nevertheless, two or three migrations deserve mention in this connection because it is clear that the problems involved in them are the same as those involved in the general study of homing. Cooke,[†] after showing that many of the birds fly by night as well as by day, takes up some of the longer routes of the birds. The longest continuous flight in the world is possibly 2,400 miles. The golden plover nests along the Arctic coast of North America and when the young have become independent the fall migration begins. The birds fly to the Labrador coast and remain there for several weeks, where food is abundant. After leaving Nova Scotia the birds fly due south to the coast of South America. The golden plover takes a straight course across the ocean and, if the weather is propitious, makes the whole 2,400 miles without pause or rest. But if tempests arise, it may be blown out of its course to the New England coast and start anew on the advent of fair weather; or it may rest for a few days at the Bermudas, one-third of the way along its course, or at the nearest of the Lesser Antilles, still 600 miles from the mainland of South America. These, however, are emergency stop-overs, to be resorted to only in case of storms. Having accomplished its ocean voyage, it passes across eastern South America to its winter home in Argentina. After dwelling 6 months in Argentina it finds its way back to the Arctic regions by an entirely different route. It travels across northwestern South America and the Gulf of Mexico, reaching the United States along the coast of Louisiana and Texas; thence it travels slowly up the Mississippi Valley and by early June is again at the nesting site on the Arctic coast.

This same bird dwells also in the Hawaiian Islands and travels from that point to Alaska, spending the winter in Hawaii and nesting in the spring in Alaska. The Hawaiian Islands are 2,000 miles from the California coast on the east, 2,400 from Alaska on the north, and 3,700 miles from Japan to the west. This is a very wonderful route, since between Hawaii and Alaska there are no landmarks.

Surprising as are these results from the golden plover, they are surpassed by the exploits of the Arctic tern.[‡] This bird dwells alternately in the Arctic and then in the Antarctic region. Their track over the 11,000 miles separating these regions is known to no one. Scattered individuals have been noticed along the United States coast south to Long Island, but naturalists have never observed these birds during migration, nor can they construct accurately the routes of the birds from the records in hand. This means that the birds probably choose an ocean route and that their flight is almost continuous.

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[*] Zoologische Jahrbücher, 1897, x, p. 238.

[†] A summary of his work appears in the National Geographic Magazine, 1911, p. 346.

[‡] According to Cooke, the Arctic tern arrives in the Arctic regions about June 15, and leaves August 25, spending thus 14 weeks at the nesting site. "They probably spend a few weeks longer in the winter than in the summer home; and if so, this leaves them scarcely over 20 weeks for the round trip of 22,000 miles. Not less than 150 miles in a straight line must be their daily task, and this is undoubtedly multiplied several times by their zigzag twistings and turnings in pursuit of food."

Several interesting points bearing upon the problem of homing come out from these studies of Cooke and others: first, that the plover and the Arctic tern have no hesitancy in undertaking ocean routes several thousand miles in length which can offer few if any landmarks in the ordinary acceptation of that term; secondly, that the birds must fly by night, which again lessens the probability that landmarks of a visual kind are used.

HOMING IN THE FRIGATE BIRD.

In regard to the homing ability of the frigate bird, the following interesting observation is cited from the *Zoological Society Bulletin* No. 29, p. 421. The article is unsigned, but was written (so Dr. Chapman informs me) by Dr. Charles H. Townsend.

> In the course of a winter's voyage on the *Albatross*, in the South Seas, the writer found, among the natives of the Low Archipelago, many tame frigate birds. The latter were observed on horizontal perches near the houses and were supposed to be merely the pets of the children who fed them. They were entirely tame, having been reared in captivity from the nest. As our acquaintance with the people developed, we discovered that the birds were used by them after the manner of homing "pigeons," to carry messages among the islands.
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> The numerous islands of the Low Archipelago extend for more than 1,000 miles in a northwest and southeast direction, and it appears that the birds return promptly when liberated from quite distant islands. They are distributed by being put aboard small vessels trading among the islands. The birds are liberated whenever there is news to be carried, returning to their perches sometimes in an hour or less, from islands just below the horizon and out of sight of the home base. Generally they are in no great hurry. As the food of the frigate bird may be picked up almost anywhere at sea, there is no means of ascertaining how much time the bird loses in feeding or trying to feed *en route*. It may also linger to enjoy its liberty with other frigate birds.
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> I did not observe tame frigate birds elsewhere in Polynesia, but Mr. Louis Becke, who is familiar with most of the South Sea Islands, says they were used as letter carriers on the Samoan Islands, when there in 1882, carrying messages between islands 60 to 80 miles apart. When he lived on Nanomaga, one of these islands, he exchanged two tame frigate birds with a trader living on Nuitao, 60 miles distant, for a tame pair reared on that island. The four birds at liberty frequently passed from one island to the other, on their own account, all going together on visits to each other's homes, where they were fed by the natives on their old perches. Mr. Becke's pair usually returned to him within 24 to 36 hours. He tested the speed of the "frigate" by sending one of his birds by vessel to Nuitao, where it was liberated with a message at $4^h\ 30^m$ p. m. Before 6 o'clock of the same day the bird was back on its own perch at Nanomaga, accompanied by two of the Nuitao birds, which, not being at their perch on that island when it was liberated, it had evidently picked up *en route*.
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> Sixty miles in 1½ hours is probably easy enough for the frigate bird, as in Malayo-Polynesia it is said to have frequently returned a distance of 60 miles in one hour. It becomes entirely tame and familiar when raised from the nest, and if given liberty returns regularly to its home-perch at night. The largest rookery of frigate birds I have seen is at Tokokoto, in the Low Archipelago.
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> Frigate birds inhabit the tropical and subtropical seas. The spread of wing is phenomenal for the size of the bird, being about 8 feet, giving wing-power perhaps unequaled.

On page 48 our own experiments on homing in the frigate bird will be considered.

HOMING IN OTHER VERTEBRATES.

Of homing in mammals little is known. We have a series of anecdotes in the literature containing probably somewhat more than a grain of truth.* We give below some of the material that has been sent to us personally from "animal lovers" over the country. We give these records for what they are worth.

The following incidents have been related concerning mammals:

(1) In May I sent my coach-dog (3 years of age) to Northampton, Massachusetts, 50 miles away. He went by carriage with my wife to Brattleboro, Vermont, 12 miles distant, and from there they took the train at 8^h 30^m p. m., in a hard rain. A closed carriage took them from the station in Northampton, where they arrived at 11 p. m. Saturday. On Monday at about 3 p. m. the dog disappeared and on Thursday about 3 p. m. he walked into our house, having been on the road 3 days. The last 12 miles he has covered a good many times, as he always goes when I drive. He evidently covered more than 50 miles, for he was seen on Tuesday near Amherst, which is not on the direct route.

(2) [A correspondent] raised a dog, crossed with hound and pointer, and littered in Lawrence. When a year old he took the young dog to Boston, got on board of a sailing-vessel, went by sea and river to Bangor, Maine, drove 40 miles into the woods at Cleveland's Camp, and hunted there two weeks, the dog proving to be a great success for quick, fast runs and returns to camp. After the hunting was over, and while on his back trip to Bangor, the dog jumped from the wagon into the bushes, having heard or smelled a deer, and went off on a hot chase. The boats ran only once in two weeks, so that, much as he valued the dog, it was necessary to go on. He took the boat at Bangor, returned by river and sea to Boston and back to Lawrence. About 2 weeks afterward the dog crawled into his yard, footsore and half starved, but safe at home and glad to get back.

(3) Some 16 or 18 years ago a young man brought to this place from his, and their, former home in Indiana two dogs of the greyhound type. Not long after they arrived here they disappeared, and in 6 weeks or so one of them arrived at his former home in Indiana, and a couple of weeks later the other one got back there. The distance is over 700 miles.

(4) I spent my vacation the past summer at my mother's, 3 miles from Siler City, North Carolina. My brother, who lived at Siler City, had a 3-months-old calf which he wanted to pasture at my mother's farm. Accordingly the calf was brought along the road from the town. The next day the animal got out of the open gate and returned home. I followed its trail—it had recently rained. The calf first took almost a bee-line for its home; crossed a small ditch, then came a large ditch, which it wandered down some distance, but returned and crossed near its direct line. This was at a distance of a quarter of a mile from the road by which it had been delivered, and all the space is covered by thick forest. When the calf struck the main road it proceeded along this to its home. This animal never had been out of its lot until it was brought to my mother's, and yet its sense of direction was so accurate that it took a straight line for home until it reached the road by which it had been brought. Then it depended upon its memory of the road, although it might have followed a path in a much more direct line.

One of my mother's neighbors, shortly after the war, moved into the State of Tennessee, 500 miles away. A dog was taken along. One day the animal was missing, and, a few weeks after, it turned up at its old home.

(5) I have a collie a little more than 2 years old. We took him with us to our camp at Point au Baril, Canada. The dog had lived in Avondale, a city suburb, all his life, and knew absolutely nothing of anything more than the ordinary suburban streets and the neighboring country fields. Our camp is on an island in the midst of a great archipelago. Every summer the people who have gone with us to the camp lose their way because the islands so closely resemble one another and are so bewildering. The dog made himself perfectly at home on our island, and although he had never swum before, he now learned

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*Observations on the homing of animals similar to those above may be found in the Revue Scientifique, 1897, made by Dusolier, p. 759, and by Artault, p. 793. Scattered through the Revue Scientifique one finds a large number of such anecdotes.

and soon developed a passion for riding in canoes, rowboats, and the steam-launch. However, he never was taken outside of the island and had possibly been 500 yards away, but not farther.

One day we took him on an excursion in a launch, some 6 miles from the camp. He was not able to see the island as we passed, because he was down in the bottom of the boat. On the return trip we got out at a little store about 2½ miles from the camp by a direct water route. Some of our boys were in a canoe at the dock, and the dog jumped into the water and tried to follow them. They did not see him, nor did we know of this until later. It was dusk, and after searching for him in vain we returned to the camp. He is a valuable dog, much beloved by all of us, and after dinner that evening we started out in canoes, went back to the store, and searched everywhere for him. We had heard that a dog (it must have been ours) had been seen swimming to the rock on which was a range light, some three-quarters of a mile from the point, but no trace was found of him there. At 11 o'clock that night the dog reappeared at the store, put his nose in at the door, and when they tried to call him he seemed frightened and disappeared in the darkness. There is a way by land from the store to our camp—6 miles of unbroken primeval country, burned-over forest with tangled swamps every quarter of a mile. It is an almost impassable territory where even the Indians get lost.

The next morning, while we were preparing breakfast, the dog appeared swimming down the channel. Our Indians insisted that he had spent the night swimming from island to island, and that when daylight came he smelled our camp—the smoke of the kitchen fire and the odor of the breakfast being prepared. At all events he made his way home, and if he swam directly from the Point it was 2½ miles by water, but if he swam from island to island it must have been a much greater distance. The channel is not direct and open, but winds in and out, and he had no knowledge of the way, so that I do not believe it is possible that he could have been guided by any landmarks.

We have taken pains to write to the contributors of each of these stories and to obtain what supplementary data we could. The incidents seem actually to have happened, but none of the contributors could state with accuracy facts enough to enable us to use the material in a scientific way.

Last summer a similar incident, with not so favorable an outcome, happened to one of the writers at his summer cottage on Stony Lake, Ontario, Canada. An 18-months-old pure-bred cocker spaniel went from the cottage to the store a mile away in the canoe with a member of the household. The store is situated on a large island containing several hundred acres. In the hurry of leaving the store the dog was left behind. After luncheon we set out to find him, first going to the store. The dog had disappeared. We then began to paddle around the island, calling the dog at every moment. We had just about given up hopes of finding him when we happened to glance at one of the small islands to the southwest of the island on which the store is situated, and in a direction almost opposite from that in which our cottage lay. There we saw the dog standing forlornly on the shore. A new house was under construction on this island and the carpenter told us that a short time before the dog had left the main island and had swum to his place. The distance from the store to the point where we found him was probably a mile and a quarter. It is interesting to note that our own cottage was under course of construction, and the fact that the dog finally landed at a place where hammering was going on might indicate that it was the sound of the hammering which made him take the direction which he did take. He probably wandered all over the large island and at some time in the course of his wandering the sound of hammering may have become audible.

Both Hodge and Fabre* give data bearing upon orientation in cats. The following account is summarized from Hodge.†

A Maltese tom cat was taken out in a row boat on one of the large Wisconsin lakes on a sultry, extremely dark night. The boat was rowed due north straight out towards the middle of the lake, which is 2 miles in width. At first the cat was quiet and then he began to get restless and extremely anxious to get home. He would climb to the end of the boat,

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*Souv. ent., II, p. 124. †Popular Science Monthly, 44, p. 758.

> stretch his head towards home, and mew continuously. The boat was turned round and round to try to throw Tom off his bearings, but to no effect. Whether right side or left, bow or stern, Tom was always on the part of the boat nearest home and straining as far as he could in that direction. Fully a mile from any shore how could he tell which shore was which? But few lights were visible and the lake is thickly wooded, and the cottages stand well back among the trees. No member of the party, except the experimenter, who used the north star for guidance, maintained orientation. Tom was wrapped up and held flat in the bottom of the boat, and then released. This likewise made no difference. He would go immediately to the part of the boat nearest home. Members of the party were blindfolded and required to guess whether the boat was turned or allowed to stand, or whether rowed in a straight line or a circle, and it was an even chance whether they guessed right or wrong. No air was stirring and no odors were detectable to the human being.

Hodge leaves the explanation in doubt, but is inclined to attribute Tom's orientation to hearing. In support of this suggestion he cites an incident connected with deer-hunting in Montana:

> While lying on the top of a hill he watched a doe as she kept guard over her two fawns. They were fully a half mile from where the observer lay. He focused his field-glasses on the group and became much interested in the alertness of the doe. "At a slight noise, occasioned by my change of position [he was of course out of sight of the deer], a noise not even noticed by myself, I was surprised to see the doe start, turn around, and point her ears in my direction. After a few minutes silence her attention was directed elsewhere, and this time I made the least "ahem"; again both ears and head were directed towards me, and so in turn for an hour I tried all manner of slight sounds—low whistles, snapping my fingers, tapping my rifle stock, scraping the ground with my foot; all were followed with the precision of response of the strychnized frog with the attent turning of the ears in my direction.

If the movements of the deer were really made in response to auditory stimuli, we would have to believe that the deer has an almost unlimited auditory acuity. It does not seem to be quite excluded, however, that the deer might have been reacting to visual stimuli, possibly through shadows, or occasioned directly by the movements of the observer. Dr. Hodge, however, does not profess to maintain that his experiment was a crucial one.

Victor Franz* maintains that fish have an extraordinarily well-developed sensitivity for detecting differences in hydrographic conditions. Currents are detected in the water by means of the lateral-line organs, temperature through warm and cold corpuscles in the skin (or through homologs), salinity through the sense of taste, depth through pressure. But Franz's paper is a *résumé* of convictions rather than a report of experiments. He argues that the spawning migration is not actuated by sexual instincts, but that it is an adaptive change which has as its end result the obtaining of optimal developmental conditions for the young. It is conditioned solely upon hydrographic phenomena.

From the above survey of the literature it would seem impossible to get any exact delimitations of the problems involved in homing. The work on the homing pigeon has been carried out in too desultory a fashion and too much under the influence of particular theories to afford satisfactory material for hypothesis. Crucial experiments designed to bring out the facts as to what the *untrained* homing pigeon can do are lacking. Until such have been made speculation on the mechanism of return is useless. In so far as any conclusions at all may be drawn from the experimental work on the homing pigeon, we may say with Exner that nothing which is done in the way of controlling the behavior of a bird (or its temporary physiological condition) on the forward journey affects its ability to return to its côte.

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*Die Laichwanderung der Fische, Archiv für Rassen und Gesellschaftsbiologie, 7, 1910, pp. 159–168.

Our own work in Tortugas has been confined largely to defining the problem of homing. We have had there an unrivaled opportunity to test the ability of *untrained* birds to home in a territory through which they have never passed, and over open-water stretches many hundreds of miles in length which apparently can offer no "landmarks." A brief account of the instinctive life of the noddy and sooty tern precedes the description of our own experimental work upon homing.

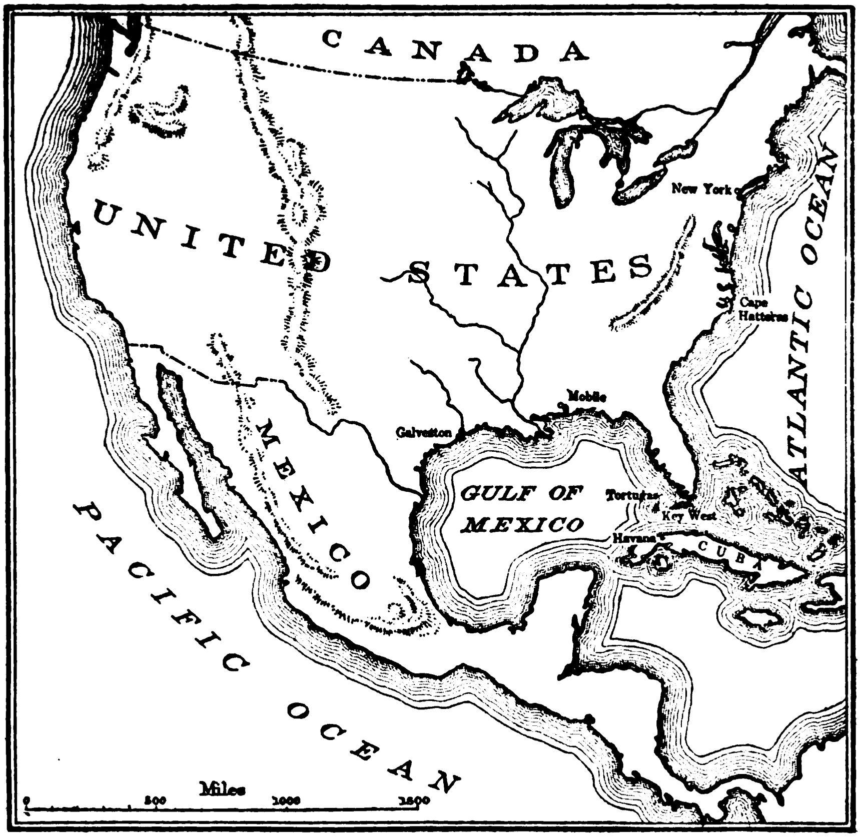

FIG. 1.—Geographical situation of Tortugas. Note the absence of land between Tortugas and Galveston

HISTORY OF THE TORTUGAS NODDY AND SOOTY TERN COLONIES.

The noddy tern (*Anous stolidus*) and the sooty tern (*Sterna fuliginosa*) are well known in tropical and juxtatropical waters. The colony which is to be found in the Tortugas from May to September was described by Audubon in 1837. He states that at the beginning of May the noddies collect from all parts of the Gulf of Mexico for the purpose of returning to one of their breeding places on one of the Tortugas called "Noddy Key." *They nearly equal in number the sooty terns, which also breed on an island a few miles distant.* He later describes the sooty tern as nesting on Bird Key. In regard to the number of sooties he says:

> As the chain grated the ear I saw a cloud-like mass arise from Bird Key, from which we were only a few hundred yards distant, and in a few minutes the yawl was carrying myself and my assistant ashore. On landing I felt as if the birds would raise me from the ground, so thick were they all around and so quick the motion of their wings. Their cries were indeed deafening, and yet not more than half of them took to their wings on our arrival, those which arose being chiefly male birds, as we afterwards ascertained. We ran across the naked beach and as we entered the thick cover before us and spread in different directions we might at every turn have caught a sitting bird or one scrambling through the bushes to escape us.

Since Audubon's time the islands have changed considerably in form. Only noddy and sooty terns (with a few least terns, which breed upon Loggerhead) breed in the Tortugas, and these appear only upon Bird Key. Furthermore, in 1907, there were 13 times as many sooties as noddies. This island is now somewhat triangular in shape and has an area of about 6,000 square yards (see plate 1; also fig. 2, p. 62). It is covered with bay-cedar bushes, cactus, and various low-growing vines (plate 2). It stands about 6 feet above mean tide level. Plate 1 gives the general appearance of the island at low tide. The small buildings were formerly used in the hospital service of Fort Jefferson. They are now used by the warden. Northeast of Bird Key, about 1¼ statute miles distant, stands the now deserted Fort Jefferson (Garden Key). In this fort is to be found a reef light about 50 feet in height. To the west of Bird Key lies Loggerhead Key, about 3 statute miles distant. This is the largest island in the group. Upon it is to be found a first-class light-house, with revolving light 151 feet in height. Certain other small islands and reefs are to be found near Bird Key. The deep waters of the Gulf of Mexico surround the group as a whole. Eastward of Bird Key, about 65.8 statute miles distant, lies Key West. Between Bird Key and the environs of Key West are found in order Rebecca Shoals lighthouse and the small islands, Marquesas and Boca Grande. On the westward side one finds only the waters of the Gulf until the shore-line of Texas is reached, Galveston being 855 statute miles distant. This strip of open water proves a magnificent route for homing experiments. Figure 1 shows the topographical relations in the Gulf region.

RÉSUMÉ OF INSTINCTIVE LIFE OF COLONIES.

In our previous paper (Watson, J. B., *opus cit.*) we gave a detailed account of the nesting behavior of the noddy and sooty. In this connection, we wish simply to supply a summary of certain of our observations bearing upon the instincts and habits which are connected directly with homing or with the control of experiments upon homing. A large amount of new material has been incorporated. This summary will deal (1) with the migration of the birds; (2) with the food and feeding instincts; (3) nesting activities; (4) swimming activities; (5) retention of nesting habits.

MIGRATION.

The time of the northern migration apparently is variable. Some statistics have been made of the approximate time of arrival at Bird Key by the warden of the Department of Agriculture and the Audubon Societies. This warden, since Tortugas was set aside as a game reserve, is present throughout the breeding season. Through the kindness of Dr. T. S. Palmer we are able to give, in table 2, the data of the time of arrival at Bird Key. It will be seen that the time of arrival is variable. The birds appear upon the island rather suddenly, noddies and sooties coming together in large flocks. They come in usually from the south and southwest. Their route is unknown. It is presumed, however, that the group leaves the Caribbean Sea and comes to the southern shore of Cuba, and then takes a northwesterly route to Tortugas.

TABLE 2.

Year.	Date of arrival.
1907	Apr. 27
1909	
1910	Apr. 27
1911	Apr. 14–May 6
1912	Mar. 20
1913	Apr. 8

The southern migration begins some time in the latter part of August and early part of September. Dr. Palmer furnishes us the dates given in table 3.

Again we see that the date for the southern migration is variable.* The birds apparently leave in flocks in a southwesterly direction. It would be interesting to know if the old birds leave first, deserting the immature birds. This seems quite improbable in view of the fact that the eggs are laid during about 4 to 5 weeks in May and early June. This means, of course, that the young birds mature from about the middle of August to the middle of September. The birds laying first would be ready to leave first with their young. Many anecdotes are told about this colony and others to the effect that the young are left by the parents and that an "enormous pilot bird" appears always in time to lead the young to their distant and unknown winter goal.

TABLE 3.

Year.	Date of departure.
1907	Sept. 22
1909	Aug. 15–27
1910	
1911	Aug. 9–Sept. 25
1912	Aug. 28–Sept. 20
1913	Aug. 29–Sept. 12

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*The impulse to migrate does not concern us in the present paper. It seems worth mentioning, however, that neither temperature nor food conditions (?) vary much from August 20 to September 20. Dr. Mayer furnished us the accompanying table of temperatures (given in degrees Fahrenheit) covering the period of August 9 to September 27. It will be seen that the average temperature is practically constant during the entire period of migration. These records tend to support the commonly accepted view that the stimulus to migration is an intraorganic one. (See Chapman, Birds of Eastern North America, p. 56.)

Date.	High.	Low.	Aver.	Extreme range for week.
1912				
Aug. 9 to Aug. 16	87.5	84	86	3.5
16 23	87	81.5	85	5.5
23 30	87.5	83	86	4.5
30 Sept. 6	98.5	84	87.5	5.5
Sept. 6 13	88	81.5	86	6.5
13 20	87.5	81	84	5.5
20 27	87	77	84	10

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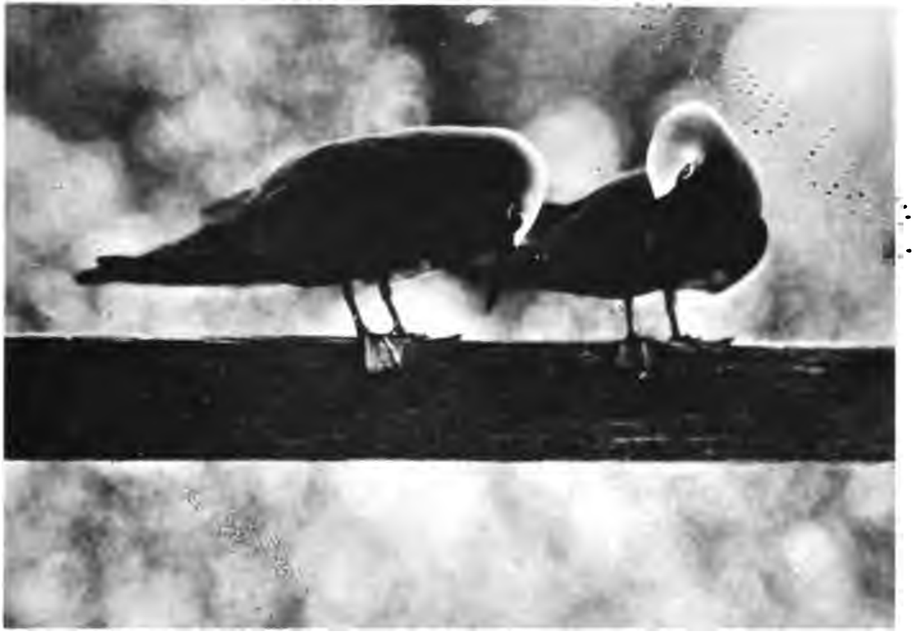

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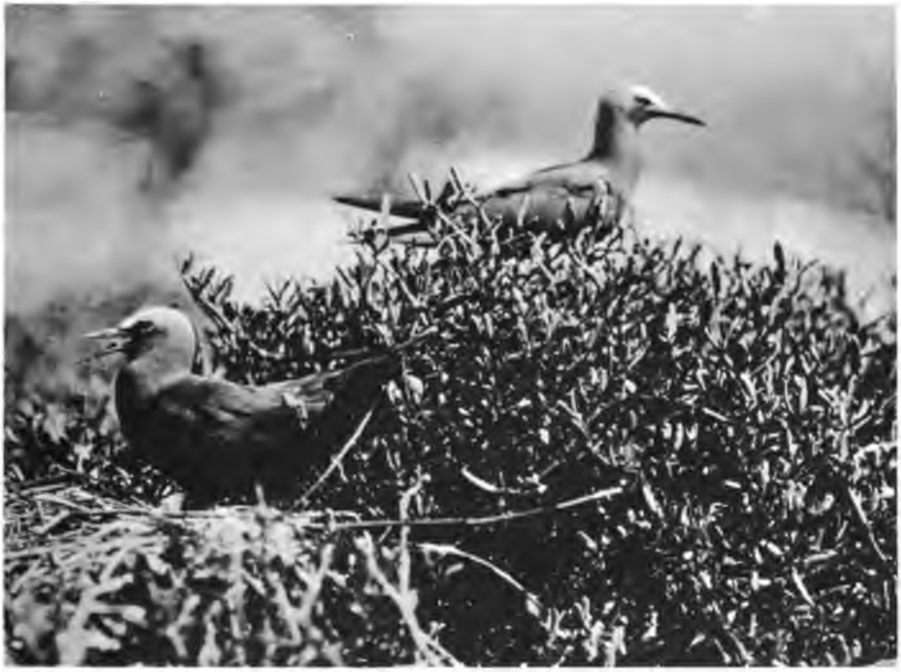

NODDY TERNS.

Fig. 1. The peculiar bowing or nodding reaction in the noddy.
Fig. 2. A typical nest with male and female in possession.

FEEDING INSTINCTS.

The noddy and sooty live almost exclusively upon minnows during the breeding-season. During the remainder of the year nothing is known of their diet. But since captive birds learn to eat cut fish with the greatest difficulty, we judge that their food, even during the winter months, is live minnows. The minnows are obtained in the following way: when large fish begin to prey upon the schools of minnows, the minnows, in their efforts to escape, spring out of the water; the birds, always hovering over the surface of the water, flock to these places and catch the minnows just as they leave the water. The following note was made on one of our trips around the island:

> *June 15, 1910:* Watched birds feeding about 2 miles out. The group comprised about 50 birds, mostly noddies. Some sooties were present and 6 least terns. The noddies hovered about 12 inches over the water, following the school of minnows. They make a rattling noise, all the while, audible 200 feet away. The noise made by any individual bird gets stronger as the fish is sighted. The noddy steps on the water often, sometimes strikes it with the breast, not in diving movements, but in those of pursuit. Never folds the wings and sits in the water.* The sooty behaves in a very similar manner, except that I saw one bird apparently diving for a fish; it certainly partially submerged its body. The least tern fishes in a characteristic way: It hovers about 6 to 10 feet above the water. The moment the fish is sighted, it folds its wings in a V shape, and shoots vertically downward, striking the water head first and going under. It does not always swallow the fish, but comes up with it in its beak. No resting on water, even with least tern; dives in an incredibly short time; comes up and is ready to strike again.

It is obvious that the tern, in order to obtain food on long trips, must be constantly in an environment both where large schools of minnows abound and where schools of large fish are constantly attacking these minnows. Furthermore, the minnow must be of a type which will spring out from the water in its efforts to escape. These peculiar conditions can be found in May (the one month when homing can be conducted) probably only in tropical and juxtatropical waters. This fact probably will always make a flight from New York, *e. g.*, impossible. On the other hand, the line from Bird Key to Galveston (Galveston being more nearly in the latitude of Bird Key) probably offers favorable feeding conditions throughout its length.

In regard to the distance from Bird Key covered by birds in their daily search for food, our 1910, 1912, and 1913 observations abundantly confirm our early (1907) observation that this distance rarely exceeds 17 to 18 miles. It may be said in passing that these birds are practically unknown both in Key West and in Galveston. Furthermore, in the many trips which we have made between Key West and New York we have never noted these birds north of Key West; hence we must conclude that Bird Key (plus 17 to 18 miles) is the northern limit of migration for both noddy and sooty.†

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*In the 1907 paper we had never seen noddies and sooties swimming in the water. In 1910 we saw one noddy fly into the water, fold its wings, and begin swimming like a duck. About 10 other noddies joined this one. This is the only occasion upon which we have ever witnessed swimming movements. We have never seen the sooty in the water, except when accident has overtaken it.

†They are reported sporadically along the eastern coast of North America. Such birds in all probability have been blown northward by heavy winds. This occurs rather frequently in the migrating period.

NESTING ACTIVITIES OF NODDIES.

The noddy tern builds its nest usually in the bay-cedar bushes, of whatever material it can find; small twigs (plate 4, fig. 1), seaweed, and shells are all used. At times the nest is placed on low-growing grasses (plate 3, fig. 2) and cacti, rarely on the bare ground. Both birds work upon the nest. Usually several days are required to complete the structure. One egg is laid. The period of incubation is 28 days. If the egg is removed, usually another egg is laid. In this way it becomes possible to prolong to some extent the breeding period.

While the nest is under construction and during the period between the completion of the nest and the depositing of the egg, the male feeds the female (plate 4, fig. 2). During all this time the birds are wild and beyond easy means of control. As soon as the egg is laid the instinctive cycle changes and the birds no longer fly out at the approach of the experimenter. At this time the noddy becomes a suitable subject for experiment on homing. At the beginning of the brooding season proper, still another marked change comes in the feeding instincts. Both birds brood the egg, shifting more or less regularly at 2 to 5 hour intervals. At night both birds are invariably present.

NESTING ACTIVITIES OF SOOTIES.

The sooty tern usually scratches out a shallow depression in the sand (plate 4, fig. 3). Since 1907 the island has become covered with a dense undergrowth and bare stretches of sand are not common. The vast majority of the eggs are now laid bare upon the earth or upon a leaf carpet. It is advisable, where homing experiments are to be carried out, to clear out this undergrowth in desirable areas. Observation of the nest is thus made easy. Clearing away the undergrowth has one disadvantage by reason of the fact that in the last few years the laughing gulls have become quite numerous on Bird Key. They persistently rob both the noddy and the sooty nests. Some means must be found for preventing their depredations. They were quite troublesome in 1913.

The sooties, like the noddies, are wild until the egg is laid (in certain nests two eggs are laid). During the brooding period they become quite bold and are easily caught. The brooding period is about 31 days. Male and female take regular turns at the nest. Shifts occur only once in 24 hours, however, and at times only once in every 48 hours. For this reason it is always more difficult in homing experiments to determine the time of arrival of the sooty at night than that of the noddy. What becomes of the sooty when not on the nest is difficult to say. The two occupants of a nest are rarely seen together. We are inclined to think, though, that both birds are near the nest at night. Close observation of the sooty is difficult unless the bird is marked. There are probably more than 18,000 (possibly 30,000) sooties on Bird Key, and the nests are often separated by a distance not greater than the length of the bird (plate 4, fig. 3). Notwithstanding this crowded condition each nest is accurately localized by its proprietors. Encroachments upon a nest or its environs by a neighboring bird are fiercely punished by the owners. The nests are carefully maintained all during the brooding period. When the young bird is 10 to 12 days of age there is a gradual desertion. The young bird runs to meet the parent and begins to feed at whatever place the meeting is effected.

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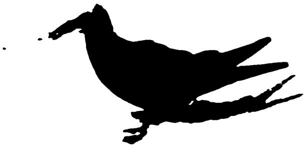

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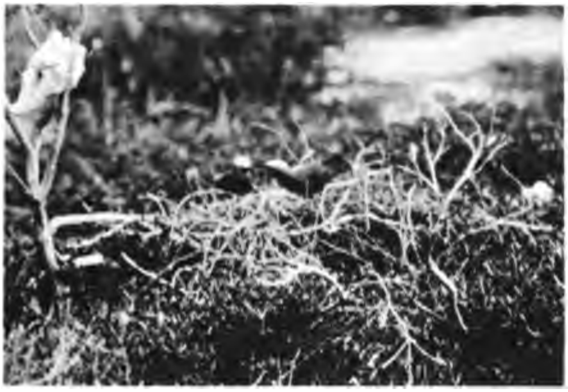

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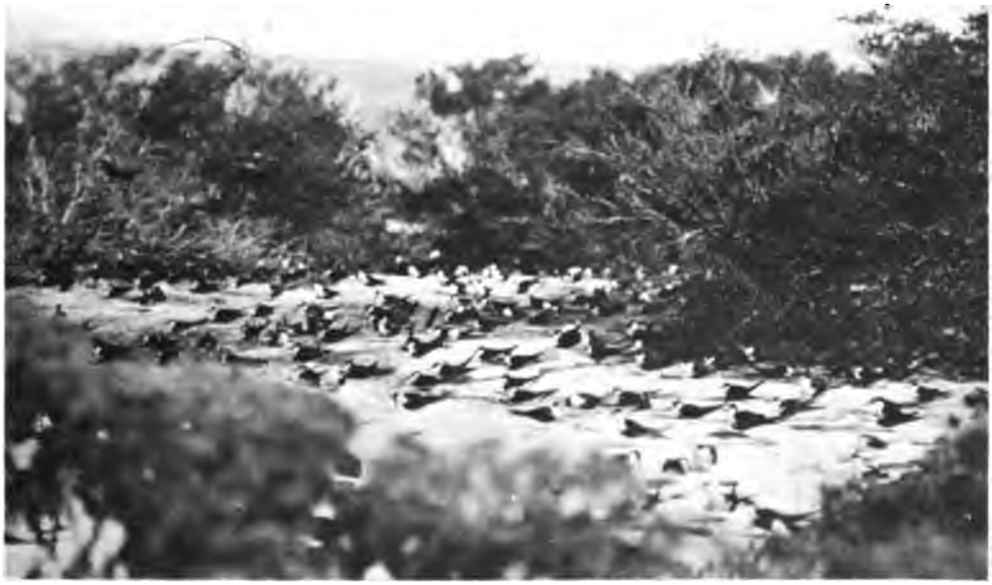

INSTINCTIVE ACTIVITIES OF NODDIES AND SOOTIES.

Fig. 1. A noddy gathering bay cedar branches. Fig. 2. Male noddy feeding female.
Fig. 3. Group relation of sooty nests.

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SWIMMING AND RESTING UPON THE WATER.

In an earlier paper we called attention to the fact that the birds during the nesting season, even while feeding upon minnows over the surface of the water, rarely come to rest in the water, and that neither the noddy nor the sooty is ever seen swimming in the water. Since, in the experiments on homing, it is necessary for the birds sent to Galveston and out over the Gulf generally to be able to pass one or more nights upon the water, it occurred to us to make some tests as to the swimming ability of the birds, their ability to rest on the water over night, etc. We report the following notes made by the senior author in 1910:

TESTS UPON THE WATER HABITS AND INSTINCTS OF NODDY AND SOOTY TERNS.

1. One noddy and one sooty were carried into the water and gently placed on the surface of the water. They arose with ease and flew away, none the worse for the test.

2. One noddy and one sooty were held in the water and at times immersed in it for a period of 10 minutes. The birds were then placed gently on the surface. The noddy immediately raised itself and flew over to the land. The sooty was helpless under these conditions. While in the water it floundered about, getting the tips of its wings out, but could not rise. Since it was becoming more and more water-logged, I rescued it and tossed it into the air. It immediately righted itself, and, gathering strength, rose higher and higher and flew away. When in the water the bird made no attempt to swim, nor did it turn instinctively towards the shore.

3. Two noddies were captured and carried into the water and plunged below the surface to a depth of 2 feet and released. When they reached the surface, both rose easily and flew away.

4. A large wire cage, 6 by 8 by 7 feet, having a 2-foot door, was carried into the water to a distance of 100 yards from the shore and left there during the test to be described. The cage was entered through a wire door in the side. It was sunk to a depth of 2 feet. This left 5 feet between the surface of the water and the top of the wire door. (See plate 5.) Two noddies and two sooties were placed in this cage at 5^h 15^m p. m. They began flying up and attempting to get out. All were able to alight on the water and to rise from it, the noddies in a beautifully coördinated way. When they alighted they would fold their wings carefully and tightly against the body and hold the head and breast high above the water, swimming as smoothly and as beautifully as a swan, and showing perfect at-homeness in the water. (See plate 5, fig. 1.) The sooties, on the other hand, arose and alighted clumsily—head barely out of the water, wings not held up—sometimes, indeed, they were spread out. The sooties, however, could swim perfectly. For about 2 hours the birds attempted to fly out, the noddies making the more vigorous resistance. The birds then became relatively quiet. I left them undisturbed until 8^h 30^m the following morning.

The noddies were in first-class condition at that time and were not in the slightest degree bedraggled or water-logged. They swam as easily and as perfectly as in the afternoon of the day before. As I approached the cage, they arose and hovered for more than a minute in the air, then alighted. I opened the door and the birds swam out and rose immediately from the water, one going at once to its nest, the other out over the water. One sooty was dead; the other was just barely able to keep its head above water; the feathers were water-soaked and the bird was shivering. Plate 5, fig. 1, shows the condition of the birds at this time. The two noddies are in perfect condition. The one live sooty is shown in the left-hand corner of the photograph. I rescued it and put in on the warm sand, where it remained and slept without moving from its tracks for nearly 2 hours. A commotion in the colony then alarmed it and it arose and started out over the water. It flew to a distance of 100 yards and fell into the water. The other birds of the neighborhood immediately began to hover over it in the peculiar way shown in our earlier study. I swam out and rescued the bird, tossing it high in the air. It flew the remaining distance to the shore and again sunned itself for more than an hour.

5. Two noddies and two sooties were put into the cage as before, this time at 11 a. m., so that I might be able to watch their behavior and rescue the birds in case of disaster. The island was generally quiet and I watched them through a field-glass so that I might not

disturb them. The birds behaved as in the previous test. After a time they ceased to make attempts to escape and settled down in the water. In about 2 hours one sooty could no longer rise from the water, and in 4 hours the second sooty became entirely water-logged. At 6 o'clock, seeing that the sooties would soon be entirely helpless, I rescued them. At my approach the noddies flew up and hovered in the air as if they had not been through any difficult experiences, and when I opened the door they swam out and flew away. The sooties were quite helpless. I took them in and kept them over night in a warm place. On the following morning they were apparently as fresh as ever.

These tests seem to show that the noddy is as at home in the water as in the air. It is quite clear that it could stay on the open water in calm weather indefinitely, and that even in rough weather it could probably last out by alternately alighting on the water and then flying up. It would seem from the above tests that the sooty would be unable to last over night in the water unless some aid were at hand. Incidental observation leads me to suppose that the sooty is the better flier. As was brought out in an earlier paper, the sooty joins the man-o'-war birds and the pelicans in difficult flying feats. These birds gathered in crowds and circled around and around, going up completely out of sight. Again at night the sooty is far more on the wing than the noddy. Furthermore, the sooty flies higher, much higher, than the noddy. In coming in at night from the water the noddy nearly always takes the lower strata, flying usually not more than a few meters above the surface. The sooty, on the other hand, flies high. Occasionally one sees two sooties darting off together and keeping parallel courses, no matter how the direction of the flight may be varied. Both wheel to the right or to the left, down or up, in a way quite similar to the evolutions of the pigeon. One never sees noddies engaged in this form of play. It would seem that the two species differ markedly in their behavior towards the two elements, air and water.

6. I became anxious to find out if the fate of the sooty forced to spend the night upon the water were changed if small pieces of drift-wood were at hand. Two noddies and two sooties were put into the cage as before. This time I had tethered against the tide 4″ by 6″ by 6″ pieces so that they floated free and were held away from each other. The sooties alighted first on the water. The two noddies began alighting on the blocks almost immediately (plate 5, figs. 2 and 3). As I write, 10 minutes later, both sooties are in the water and both noddies on the blocks. The blocks keep turning over in the water, since the tide is running out rapidly and it is hard for the birds to keep their footing. The sooties make little or no effort to take the other two blocks. They sometimes fly up in the air, but rarely attempt to take the blocks. One just caught the block (plate 5, fig. 2), but flew up immediately and did not again attempt to alight on it. The noddy when alighting goes always to the block. At the end of the first ten minutes one sooty began constantly to climb up and ride on the block but could not stay on very well. The other sooty had not made the slightest attempt to alight on it. The noddies at the end of twenty minutes never alighted on the water. At the end of 25 minutes one sooty, which had been constantly in the water, was no longer able to rise from it (plate 5, fig. 4). Two hours later the bird which was unable to rise escaped by reason of the fact that the tide had dropped below the top of the door in the side of the cage, which I had neglected to close. The other three birds each possessed a block and were calmly standing upon it, making no efforts or struggles to escape. At 1^h 15^m the sooty had perfectly mastered the block and seemed quite content. It apparently had to learn to use the block and did not go instinctively to it. At 2 p. m. I captured another sooty and placed it in the cage. The behavior of this bird was wholly similar to the above. Its efforts disturbed the other sooty, which began to make struggles to escape, becoming uncoördinated in its movements, and finally dropping into the water. At 4^h 30^m both sooties were in such poor condition that I decided to release them. The noddies were still in as good condition as before.

7. On June 9, I tethered heavy pine boards 1″ by 6″ by 8″ as floats. They were fastened at both ends, so that no matter which way the tide was running they would remain relatively stable. Under these conditions the sooties passed the night comfortably and were in perfect condition on the following morning.

It seems quite clear from these experiments that if the sooty could find fairly heavy pieces of drift-wood in the Gulf or beds of sea-weed, which are probably always present, it would be able to pass an indefinite period of time upon the water. Up to the 1913 experiments I had supposed that this inability to pass

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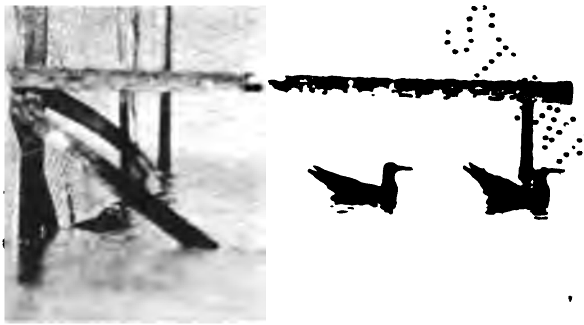

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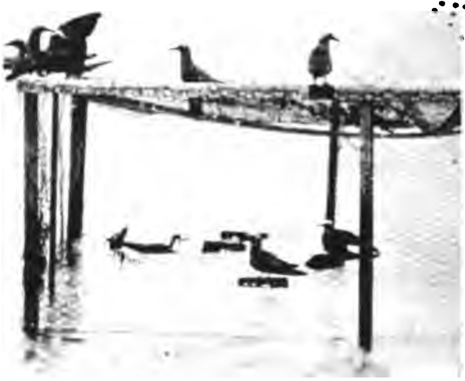

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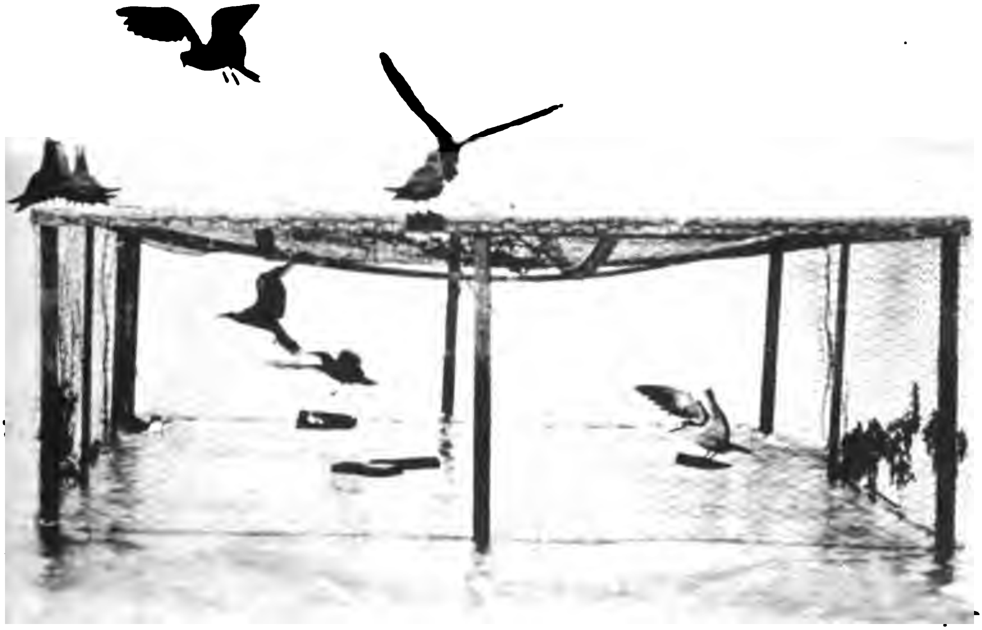

METHOD OF TESTING SWIMMING BEHAVIOR.

Fig. 1. Noddies and sooties after spending night on the water. The two noddies are in good condition. One sooty is drowned and the other is shown, in lower left hand corner, in a very poor condition.

Fig. 2, 3. Illustrating the noddies' quick possession and retention of the blocks. The sooties have left the blocks and are slowly becoming water-logged.

Fig. 4. The test with floating blocks. One sooty failed to use the block and is in poor condition.

the night upon the water in the absence of drift-wood accounted for the failure of many of the birds to return to Bird Key. The 1913 experiments upon homing between Galveston and Bird Key (p. 54) seem to show that entire reliance can not be placed upon the results of the experiments we have just considered. In the Galveston tests many of the birds were out upon the water (apparently) during periods ranging from 5 nights to 17 nights. Hence we must conclude either that drift-wood was abundant or else that the sooty when not confined can spend the night upon the water. If our results are taken at their face value they would seem to force the conclusion that the Galveston sooties were able to find something to rest upon during the night.

RETENTION OF NESTING HABITS.

In controlling experiments upon homing it becomes essential to know (1) the length of time the bird left on the nest (O) will care for the nest, egg, young, etc., and (2) the length of time nest habits will be retained by the bird which has been sent away (R). The necessity for data on (1) arises by reason of the fact that as soon as the bird left at home begins to desert the nest, other birds steal the straws, if it is a noddy nest, or fill it with sand, disarrange the egg, etc., if it is a sooty nest. Nests so disturbed will not be taken by birds returning from the experiments on homing. Since the observer can not keep all of the nests under observation at any one time, it is essential that they be kept in good condition by the bird remaining at the nest. In order to control this factor perfectly it would be advisable in future experimentation to invert wire cages (with open doors) over the nests several days before capturing the birds which are to be sent from the island. These nests could be watched and as soon as the O at any given nest begins to desert, the door of the cage could be closed up until R was expected. R having been habituated to the cage before he left, would not hesitate to enter it on his return if the door were left open or to perch upon it if the door were closed.

The necessity for data on (2) appears when we consider the possibility of the effect of loss through disuse (or waning) of nest habits, upon the possibility of locating the bird (R) upon its return. If nest habits, habits formed to a particular nest, to mate, etc., are lost at the end of 2 or even 3 weeks, it is unlikely that the total number of birds returning from long trips can ever be observed. Fairly complete data have been gathered upon (1).

OBSERVATION UPON BEHAVIOR OF BIRD LEFT AT NEST (O) AFTER REMOVAL OF NEST MATE (R).

So many observations have been made upon this phase of the subject, that only a small number of our records will be given. We present in table 4 the behavior of 24 birds whose mates had been sent to Galveston. The mates were removed May 15, 1913. During the first 6 days the O's carefully guarded the nests, usually sitting closely upon the eggs. Occasionally short trips for food and water were made. This, in the case of the sooties, means a tremendous change in habits, since they ordinarily leave the nest for 24 hours at the nest shift.

Records similar to the above were kept upon several different occasions, but the results were identical. Summarizing (1), we find that both noddies and sooties, when left alone at the nest, remain on guard and brood the egg closely for at least 6 days. There then ensues usually a period where, in most cases, the birds begin to guard the egg less closely, leaving it entirely for long stretches of time, and on returning merely stand or sit near it. Complete desertion finally occurs. Individuals differ greatly as regards time of desertion, as may be seen by examining table 5, condensed from table 4.

TABLE 4.—*Behavior of 24 birds whose mates had been sent to Galveston.*

A = absent. P = present. MR = Mate returned. Pa. = Present but not sitting on nest. D = deserted. CAM = courted by another bird.

	7 days.	9 days.	11 days.	14 days.	19 days.	22 days.	27 days.	Remarks.
Sooties.								
No. 1	A	A	A	MR	..	..	..	Both birds hung around nest but never completely resumed care of egg.
2	P	A	A	P	Pa.	D	D	Deserted completely.
3	P	A	A	A	D	D	D	Deserted completely.
4	P	A	P	A	P	D	D	Deserted completely.
5	P	P	P	P	MR	..	..	The pair completely resumed nesting activities.
6	A	A	A	P	P	Pa.	D	Very faithful to end of observation.
7	P	A	A	P	A	D	D	Deserted.
8	P	P	A	MR	..	..	..	Pair resumed nesting activities.
9	P	P	MR	..	..	..	..	Pair resumed nesting activities.
10	P	P	A	MR	..	..	..	Pair resumed nesting activities.
11	P	A	P	MR	..	..	..	Pair resumed nesting activities.
12	A	A	A	MR	..	..	..	Completely resumed nesting activities, although had apparently deserted.
Noddies.								
No. 13	A	P	P	P	Pa.	D	D	Deserted.
14	P	P	P	A	Pa.	MR	..	The pair completely resumed nesting activities.
15	P	A	P	P	A	D	D	Deserted.
16	P	Pa.	A	P	A	D	D	Deserted.
17	P	A	P	P	D	MR	..	Deserted, but R when he returned took another nest mate and resumed (incompletely) nesting activities.
18	P	P	CAM	MR	..	..	..	Nesting activities not resumed.
19	P	P	P	P	A	P	P	Faithful to end of observation.
20	P	P	MR	..	..	..	..	Pair resumed nesting activities.
21	P	P	Pa.	A	D	..	..	Deserted completely.
22	A	Pa.	MR	..	..	..	..	Pair completely resumed nesting activities.
23	Pa.	CAM	D	..	..	..	..	Deserted.
24	P	P	P	MR	..	..	..	Completely resumed nesting activities.

TABLE 5.

No. 2 deserted at end of 19 days.
3 deserted at end of 7 days.
4 deserted at end of 19 days.
6 did not desert during limits of observation (27 days).
7 deserted at end of 14 days.
13 deserted at end of 19 days.
No. 15 deserted at end of 14 days.
16 deserted at end of 19 days.
19 did not desert during limits of observation (27 days).
21 deserted at end of 14 days.
23 deserted at end of 11 days.

Only birds whose mates did not return are listed in this table. The data in all of these studies on retention of the nest suffer by reason of the fact that sex was not determined. No. 23, deserting at the end of 11 days, was undoubtedly a female.

RETENTION OF NESTING HABITS AND NEST LOCALITY IN THE BIRD REMOVED FROM THE NEST (R).

In order to test the limits of retention of nest locality, 10 noddies and 10 sooties were captured and their nests plainly marked on May 12, 1913. They were individually marked with oil paints, carried to Loggerhead Key, and kept in a large fly-, mosquito-, and ant-proof cage.* We planned to release these birds at varying intervals and to note whether they returned and resumed normal nesting activities with their mates. The experiment was planned to give the limits of time within which complete resumption of nesting activities might take place after forcible detention on Loggerhead. The test was completed as follows: On the day any given bird was to be released on Loggerhead the experimenter stood before the nest while an assistant took the motorboat and went to Loggerhead to release the bird. The watches of the experimenter and the assistant were set together. The following summary is taken from the notes of one of the observers.

11 days:

Noddy No. 11 was released at $4^h 24^m$ p. m. after spending 11 days in captivity. Upon release at Loggerhead the bird flew out to water and thoroughly bathed. Thereupon it flew off straight to Bird Key. Bird was fed before leaving. Arrived at rim of nest at $4^h 34^m$. Total time 10 minutes. Flew away an instant after alighting. No sign between mates was made. O had been very faithful. Upon R's return did not attack, as it surely would have done had R been a stranger. After 26 minutes R returned to island and flew to house top. Remained there 8 minutes, then came down and arriving at nest bowed (plate 3, fig. 1) to mate. Mate bowed in return. R did not sit on egg that day, but brooded it the following day in a normal manner.

15 days:

Noddy No. 17 was released at $11^h 33^m$ a. m. after 15 days. Arrived at nest at $11^h 57^m$. Time, 24 minutes. Left nest and did not reappear before observer left at $1^h 15^m$. O was not on the egg but on nearby limb. Bird did not appear again that day while I was present. On the following morning I saw O repeatedly drive R away. Friendly relations were never resumed.

Sooty No. 12 was released at the same time. This bird never appeared at its nest.

16 days:

Noddy No. 18. Released at 5 p. m. after 16 days. Would not leave Loggerhead. Flew to water, thereupon to bow of one of the boats, then underneath dock. Finally disappeared from Loggerhead but never appeared at its nest.

Sooty No. 5. Released at same time as No. 18. Flew out over gulf to Southwest, then turned and started towards Bird Key. Never was observed at nest.

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*Very fine galvanized wire netting inclosed all sides of the cage. The cage was floored and covered with wooden boards. It was mounted upon four legs, 3 feet in height, and the bottoms of the legs were inserted into large pails kept filled with water. Fresh sand was kept on the floor of the cage. The birds were fed with minnows. At first they would not eat and some had to be forced to eat. After 4 or 5 days the majority of them began to eat. For some reason many of the birds lost flesh rapidly and died, even in cases where they apparently ate the normal number of minnows. Of the 20 birds in captivity only 13 lived through the experiment.

18 days:

Noddy No. 16. Released at $9^h\ 30^m$ a. m., 18 days in captivity. Refused at first to leave dock. When driven away started north after bathing. Was not observed at nest until 6 days later. He was then sitting on the rim (at 5 a. m.). Mate was near. Nesting activities not resumed. Probably on Bird Key on night of day released, but left for feeding-grounds every morning before observations could be made.

Noddy No. 19. Released same hour as No. 16. On release joined No. 16 in flight. Seen near nest on following morning. Nest not resumed. Mate had completely deserted.

20 days:

Sooty No. 7. Released $8^h\ 50^m$ a. m. after 20 days. Bird very weak. Would not leave Loggerhead and finally died there.

Sooty No. 8. Released as above. Flew off and headed north. Never appeared at nest.

22 days:

Noddy No. 20. Released $3^h\ 31^m$ p. m. after 22 days. Flew north. O had taken another mate. R was not observed until 3 days later (probably was driven off by O). When observed R was not sitting egg. Nest was finally abandoned.

25 days:

Noddy No. 13. Released 8 a. m. after 25 days. Not observed at nest until 3 days later. Made no effort to sit egg. O not near nest.

Noddy No. 14. Released with No. 13. Spent 5 minutes in water, then flew west. In good condition. Not observed until 3 days later. Mate not near. Made no effort to sit egg.

26 days:

Noddy No. 15. Released 11 a. m. after 26 days. Spent 5 minutes in water, then flew west, appearing at nest at $12^h\ 30^m$ p. m. Was not sitting on egg. Two days later was observed sitting on limb above mate. Mate was on the egg. Later observations showed that O had accepted another mate. R often appeared and hung around, but never forced out the intruder.

A summary of these field notes is given in table 6:

TABLE 6.

No. 11 at end of 11 days returned to nest.
17 at end of 15 days returned to nest.
16 at end of 18 days returned to nest.
19 at end of 18 days returned to nest.
20 at end of 22 days returned to nest.

No. 13 at end of 25 days returned to nest.
14 at end of 25 days returned to nest.
15 at end of 26 days returned to nest.
18 did not return to nest after absence of 16 days.

None of the 4 sooties living through the experiment returned to the nest.
Except No. 11, the relations with mate were not resumed.

From this series of notes we see either that the conditions were not favorable to the sooties or else that locality and nesting habits are not retained by them for as long a time as by the noddies. From data offered below it would seem that the unnatural conditions offered by captivity at Loggerhead produced a waning of the nesting impulses, if not loss of retention of nest locality, and furthermore, that habits of responding to a given mate are lost before the habits of responding to a given nest (place). The system of observation at the nest, however, had not been perfected. When hundreds of nests were under observation by one investigator, it might easily have been possible for him to have timed his observations in such an unfortunate way as to have missed the appearance of the Rs at the nests. A reference to page 42 shows that the sooty when not brooding the egg disappears for 24 hours and sometimes 48. Furthermore, these birds usually leave their nests at daybreak, before there is sufficient light for identification.

Data supplementing the above may be obtained by referring to table 4, p. 42, which gives a record of 13 birds returning from the Galveston trip (places are marked by the words "mate returned"). The length of time the birds were out is given in table 7.

TABLE 7.

Sooty No.	1 returned after 14 days.	Noddy No.	14 returned after 22 days.
	5 returned after 19		17 returned after 22
	8 returned after 14		18 returned after 14
	9 returned after 11		20 returned after 11
	10 returned after 14		22 returned after 11
	11 returned after 14		24 returned after 14
	12 returned after 14		

In this test, where the birds were not held in captivity, we find 7 sooties returning to the nest after intervals varying from 11 to 19 days and 6 noddies after intervals varying from 11 to 22 days. In most cases where the nest had been maintained by Os, the Rs on *returning resumed normal nesting activities with their former mates.* We thus see that under these more natural conditions the nesting impulse remains strong from 2 to 3 weeks and that the habits of reacting to a particular nest and nest mate are also retained during this period.

The question arises, of course, as to how many birds returned to Bird Key after the various expeditions but escaped observation through the *waning of the nesting instincts or the loss of nest habits.* This question is not wholly answered by our experiment. It seems improbable that birds returning under 2 weeks could have escaped observation. If return was delayed much longer than this (as was perhaps the case in many instances) it is probable that the presence of the birds at the nest was too sporadic to be detected by non-continuous observation.

GENERAL TECHNIQUE OF THE HOMING EXPERIMENTS.

The following routine was adopted on Bird Key in preparing for an experiment on homing. Roads were first cut through the thickly populated noddy and sooty districts. These roads may be cut at any time before May 15 (they should not be cut later than this because of the number of eggs which are on the ground). It is easy to capture both noddies and sooties on these roads, and easy to observe their return. Where, in the course of a season, so many birds are likely to be on the road, it makes it very much easier to take all of the Galveston birds, *e. g.*, from one road, the Key West birds from another, etc. As one passes down the roads the boldest of the birds will stay on the nests, or if they do leave momentarily, they will fly back while the experimenter is standing close to the nest. These bold birds are the ones always captured. Before passing down the road for the purpose of capture, stakes about 12 inches long and 1 inch square are made. A large Dennison tag and a small tag are attached to the end of the stake, the small tag being attached loosely. The two tags bear identical legends. The large tag will have written upon it in water-proof ink, *e. g.*, "Sooty, Galveston, removed May 16, marked with scarlet lake, 3 bars on head and neck." When the bird is captured the stake is pushed down into the sand if a sooty or tied to a convenient twig if a noddy very near to the nest (plate 6, figs. 1 and 2). The small tag, bearing a duplicate of the above legend, is pulled off. The bird and small tag are handed to an assistant, who ties the tag around the bird's neck and puts the animal in a portable cage. When enough birds have been collected the lot is taken back to the house and marked with oil paints as indicated by the cards attached to the birds' necks. Plate 6, figs. 1 and 2, show also the clearness with which the markings appear after the return of the bird. Not until 1913 did we realize the importance of having individual compartments of large size in the carrying cage, and although we used individual compartments in 1913 they were not large enough, so that it may safely be said that none of the experiments to be reported has been carried out under ideal conditions. Certainly if any other work is ever to be attempted at Bird Key it is absolutely essential to have a large compartment for each bird, and a supply of minnows sufficient to last the whole trip. The most convenient way to perfect the technique of feeding the birds on the trip is to send a refrigerator with the birds and to keep the minnows stored in this.

PREVIOUS EXPERIMENTS ON HOMING AT TORTUGAS.

In order that the present paper may give a complete record of the homing work done at Tortugas, we copy the following summary from the 1907 publication.

Experiment I.

Six noddies were captured one evening and marked characteristically and individually with oil paints. These birds were put on board the laboratory launch, which happened to be making a trip to Key West on the following morning. The nests of these birds were all close together and were tagged with a large card in order to facilitate observation. Two of the birds were released at Rebecca Shoals Light, 31.38 km. (19.5 statute miles) from Bird Key; two at Marquesas, 72.75 km. (44.75 statute miles); and two at Key West, 106.02 km. (65.8 statute miles). I kept their nests under constant observation the whole day long. Naturally, since the birds had been without food for some time, and since I had no guarantee that they would immediately seek the nest after reaching the island, I expected the return to the nest to be irregular. The results were as follows:

The two Rebecca birds, released at $9^h\ 30^m$ a. m., returned about 12 noon.

The two Marquesas birds, released at $2^h\ 15^m$ p. m., returned together at 4 p. m.

The two Key West birds were released at $6^h\ 30^m$ p. m. One returned at $7^h\ 30^m$ a. m. the next day, the other at $5^h\ 05^m$ p. m. These two birds, bearing out my statement that these terns do not fly at night, probably slept in the neighborhood of Key West and left early the next morning. A heavy gale and rainstorm set in very shortly after these birds were released and I doubted very seriously whether they would ever return. Apparently one of the birds was not affected by the storm, while the other was probably blown from its course. The respective mates of these birds remained on the eggs the entire time, going neither for food nor water (?).

Experiment II.

Three noddies and two sooties (one of the sooties was known to be a male) were captured and marked as above. Their nests were likewise prominently marked. On the early morning of Thursday, June 13, these birds were put into a large insect cage and given in charge of Dr. H. E. Jordan, who was returning to New York. He carried these birds *via* the government tug to Key West. There food was purchased for them (minnows). At 3 a. m. Friday the 14th, Dr. Jordan boarded the Mallory boat *Denver*, which left at that time for New York. On board the boat the birds were both watered and fed. On Sunday, the 16th, at $9^h\ 20^m$ a. m., the birds were released at lat. 35° 8′, long. 75° 10′ (12 miles east of Cape Hatteras, approximately). The wind was fair for several days after the birds were released. I kept their nests under constant observation, but had almost given up hope of their returning when, to my surprise, on June 21, at $8^h\ 30^m$ a. m., I found both marked sooties on their respective nests.

None of the marked noddies was ever found on its old nest, but several days after the sooties had been observed at their nests, by chance I observed one of my marked noddies attempting to alight on its nest. On account of the mate having formed new "affiliations" this was not permitted, and I immediately lost track of the bird. I have little doubt that the other noddies also returned to the island, but likewise were not permitted to return to their nests.

The distance from Hatteras to Bird Key in a straight line is approximately 1,367.9 km. (850 statute miles). The alongshore route, which is the one in all probability chosen by the birds on their return, since they were gone several *nights*, is approximately 1,739.6 km. (1,081 statute miles).

EXPERIMENT III.

On Monday, July 8, two noddies and two sooties were captured and marked and given into the charge of Dr. Robert Hartmeyer, who was returning to Germany by way of Havana. The birds were in such poor condition, owing to the enormous strain of several days' feeding of their then quite large young, that we decided to release them at Havana instead of taking them farther out. On the 9th the birds were carried by Dr. Hartmeyer on board the government tug and taken to Key West, where they spent the night and part of the following day, the 10th. They were carried in Dr. Hartmeyer's stateroom to Havana on the night of the 10th. Early in the morning of the 11th the birds were released in Havana Harbor. All returned to Bird Key on the 12th. Since they had had to spend 3 days without food or water, they were in poor physical condition. They probably spent one day and night around the shores of Cuba, leaving there early in the morning of the following day. The noddies were observed on their nests at 7 a. m. while the sooties were noted for the first time at $6^h\ 30^m$ p. m. of the same day.

The distance in a straight line from Havana to Bird Key is approximately 173.8 km. (108 statute miles).

RECORD OF EXPERIMENTAL WORK ON HOMING IN 1910 AND 1913.

THE FLIGHT FROM KEY WEST.

On May 16, 1910, 12 noddies, 12 sooties, and 4 man-o'-war birds were captured and marked individually as described below. We had intended to ship these birds to Key West on the 17th in order to send them to Galveston on the 18th by Dr. J. F. McClendon.* On the 17th a heavy storm set in and the naval tug could not leave Tortugas. On the 18th, since there was still a chance to catch the Galveston boat, they were carried by Dr. McClendon to Key West. The tug arrived too late to connect with the Galveston boat and the birds were accordingly released May 18 at $2^h\ 30^m$ p. m. in Key West Harbor, 65.4 knots

TABLE 8.—*Flight of noddies from Key West.*

Marking.	Returned.	Days out.
Yellow, irregular splotches on right wing	May 20, noon	1 d. 21½ h.
Yellow band encircling neck	May 20, $10^h\ 30^m$ a. m.	1 d. 20 h.
Yellow line between wings	May 21, 6 a. m.	2 d. 15 h.
Yellow, irregular splotches, right wing	May 19,[1] 10 a. m.	19½ h.
Yellow, solid on right wing	May 19, 5 p. m.	1 d. 2½ h.
Yellow, two vertical lines on head	May 19,[1] 8 a. m.	17½ h.
Yellow line from apex of head down to tail feathers	May 19,[1] 8 a. m.	17½ h.
Yellow, splotched head and neck	May 19,[1] 8 a. m.	17½ h.
Yellow, two heavy vertical bars on head and neck	May 19,[1] 10 a. m.	19½ h.
Yellow, solid on head	May 20, $10^h\ 30^m$ a. m.	1 d. 20 h.
Yellow, solid on left wing	May 20, 8 a. m.	1 d. 17½ h.
Yellow, horisontal lines on head	May 19,[1] 8 a. m.	17½ h.

[1] These birds probably returned afternoon of day before, *i. e.*, same day released. All the birds had a strong northeast wind with them.

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*I am very grateful to Dr. McClendon for his help in this experiment.

due east of Bird Key. Thinking that Dr. McClendon had made the Galveston boat, we did not visit the nests that afternoon. On the following morning, in making the rounds of the nests, we observed several of the marked birds on their nests. We began then to make systematic observations and report here the first time each bird was observed at its nest. In all cases these are the actual first observances of *appearance on* the nest, but in view of what has been said earlier (p. 45) it is possible that the birds may have attempted on earlier occasions to take possession of the nest. Tables 8 and 9 show the time of release, the markings of the bird, and the apparent time of return.

On June 10, at 2^h 30^m p. m., 1 man-o'-war bird was observed. That the others were not observed is not remarkable, since:

(1) There was no adequate stimulus to cause them to return. The man-o'-war bird is at home on any coast or island south of Hatteras. He merely acts as a scavenger wherever he may find himself. The results might be quite different if we were to carry out similar experiments upon him in the Bahamas at the time of the nesting season or were to rear these birds as pets.

TABLE 9.—*Flight of sooties from Key West.*

Marking.	Returned.	Days out.
Scarlet lake, two circles on breast........................	May 24, 6 a. m.	5 d. 18½ h.
Scarlet lake, three horizontal dots on breast..............	May 25, 6 a. m.	6 d. 18½ h.
Scarlet lake, three diagonal dots on breast.................	May 19, 8 a. m.	17½ h.
Scarlet lake, three horizontal bars on neck and breast.......	May 20, 8 a. m.	1 d. 20½ h.
Scarlet lake, solid red breast.............................	May 19, 8 a. m.	17½ h.
Scarlet lake, three vertical dots on breast.................	May 19, 8 a. m.	17½ h.
Scarlet lake, irregular lines on breast.....................	May 20, 8 a. m.	1 d. 20½ h.
Scarlet lake, diagonal lines, left to right on breast..........	May 27, 6 a. m.	8 d. 18½ h.
Scarlet lake, large splotches on breast (male)..............	May 28, 6 a. m.	9 d. 18½ h.
Scarlet lake, diagonal line, right to left on breast..........	May 30, 3 p. m.	11 d.
Scarlet lake, three horizontal bars on breast...............	....	....
Scarlet lake, three vertical lines on breast................	....	....

(2) The second difficulty lies in the fact that many of the birds are deeply hidden by the bushes. For some reason not yet found out they line the edges of the bushes wherever the terns are nesting; we now suspect for the purpose of collecting the eggs and young. They often roost and rest quite low and it is impossible to cover the whole island adequately with the glasses. Even if the other birds did return, the chances are much against the fact being discovered.

Before the above 4 birds were released, 2 man-o'-war birds were released by Dr. Mayer in Key West, on May 6, at 2^h 13^m p. m. One of these birds returned on May 11. We happened to get close enough to observe him without the aid of glasses. On account of the difficulty of noting their return, future work with them was discontinued.

The records that the terns made in this Key West flight are valuable in view of the fact that they show that the birds, when covering *short distances, require,* in *many cases, as much time as birds covering longer distances.* In the above tables the time ranges from 17.5 hours to 11 days. Many of the returns from distances greater than 500 miles did not require more than 3 to 5 days (pp. 50 and 58).

As this Key West flight gave us a set of "trained" birds, we tested the speed at which the noddy and sooty can fly, as follows: 3 noddies and 1 sooty, which had already flown from Key West on the above flight, were again captured and sent in a hooded cage to Key West; they were released in Key West harbor at 2 p. m. (See table 10.)

TABLE 10.

Birds.	Time.	Remarks.
Noddy 1	$5^h\ 45^m$	All birds returned together. They came in with a great flock of other birds which had been feeding on the open water (the return of the birds in large flocks is usual just at nightfall). The birds probably made good time until the feeding-ground was reached, and then leisurely ate. It would be a far better test to take well-fed birds and release them about 5 p. m. Owing to an oversight this test was not made in 1913.
Noddy 2	$5^h\ 45^m$	
Noddy 3	$5^h\ 45^m$	
Sooty 1[1]	$5^h\ 45^m$	

[1] The young bird was present in the nest of this sooty.

Since Bird Key is only 65.4 miles from Key West, the time ($3^h\ 45^m$) is not very rapid when compared with that in which the homing pigeon could cover a short distance like this (at the rate of 1,200 to 1,600 yards per minute).

ATTEMPTED FLIGHT FROM NEW YORK AND EN ROUTE.

On the afternoon of May 19, 1910, birds for a New York–Tortugas flight were captured. They were taken to Key West, leaving the island at 8 a. m., May 20, on the *Vellela*. It was stormy and the *Vellela* got into Key West too late to catch minnows for the trip. While we felt sure that this doomed the expedition to failure, nevertheless we purchased a large fish, which we cut up into strips, substituting it as a food supply in place of the minnows. The Mallory boat *Concha* left Key West harbor the night of May 20 at $10^h\ 30^m$, the birds being in charge of Mr. Wilson. The cage was hooded and in addition was carried in the hold of the vessel. The first lot of birds was marked as shown in table 11.

TABLE 11.—*Night release.*

Sooty No. 1.	Yellow, line down back, 1 dot on breast.
Sooty No. 2.	Yellow, both wings splotched.
Sooty No. 3.	Yellow, right wing splotched.
Sooty No. 4.	Yellow, 3 vertical bars on left wing.

These 4 birds were released at $7^h\ 30^m$ p. m., 365 miles from Bird Key, *at night* (immediately after twilight had disappeared). Only 1 bird from this lot returned, requiring approximately 4 days. On release, 1 of the 4 birds started due south and the others southeast. The weather was fair until the 24th. On the evening of the 24th a heavy southeast wind set in, which made it impossible for the birds to make Bird Key. The rest of the birds were carried to New York. They were marked as shown in table 12.

TABLE 12.—*Released in New York harbor.*

Sooty:		Noddy:	
No. 1.	Yellow, solid breast.	No. 1.	Red, solid head.
2.	Yellow, one vertical bar on breast.	2.	Red, vertical bar on head.
3.	Yellow, one large horizontal bar on breast.	3.	Red, one horizontal bar on head.
4.	Yellow, two large horizontal bars on breast.	4.	Red, right wing and head solid.
5.	Yellow, vertical bars on breast.	5.	Red, left wing and head solid (died in passage.)
6.	Yellow, splotched breast.	6.	Red, splotched head.

On account of the food conditions the birds became weaker and weaker. They were released in New York harbor on Tuesday morning, May 24, at $4^h\ 30^m$, in a fog. On release they left the ship and flew to a distance of 200 yards, alighting in the water. One sooty was too weak to maintain itself in the air. These birds probably would have had to fly 1,000 miles before they could find a suitable fishing-ground. As has been mentioned, they eat only live minnows, which hop over the surface of the water. In view of this fact it is not surprising that none of the birds returned to Bird Key. Furthermore, the spring in 1910 was much delayed. The air and water in New York harbor were unusually cold, but the other weather conditions at first were favorable. There were south and southeast winds on the 24th and 25th, while a heavy northeast wind with squalls began on the 26th and continued through the 27th. From May 28 to June 1 a flat calm prevailed. On the 1st of June a heavy south wind set in.

THE FIRST GALVESTON TRIP, 1910.

The birds as marked below were captured and put into a hooded cage on the afternoon of May 29, 1910. They were carried to Key West on the *Physalia* May 30, and put on board the Mallory boat *Concha*, leaving Key West in the afternoon of June 1, in charge of Mr. Wilson. Two releases were made. The birds in the first release were marked as set out in table 13.

TABLE 13.—*First release.*

Noddy:		Sooty:	
No. 1.	Yellow, one horizontal bar on head.	No. 1.	Red, one horizontal bar on breast.
2.	Yellow, two horizontal bars on head.	2.	Red, two horizontal bars on breast.
3*	Yellow, one vertical bar on head.	3.	Red, one vertical bar on breast.
4.	Yellow, two vertical bars on head.	4.	Red, two vertical bars on breast.

These birds were released June 3 at $4^h\ 45^m$ a. m., *en route* for Galveston, in the open ocean. The *Concha* was then 470 knots from Key West. Since Bird Key is 60 knots from Key West that distance must be subtracted, leaving a distance from Bird Key of 410 knots, or approximately 461 statute miles. On release all birds with one exception started east. That one headed west and continued for about 200 yards, then turned suddenly and started east. The birds all flew up about 20 to 30 feet, then downward, and started off within a few feet of the water.

The returns were as follows:

Noddy No. 1 returned night of June 6; time, 3 days.
Noddy No. 4 returned night of June 6; time, 3 days.
Since Noddy No. 3 died we have 2 noddies out of 3 returning from this trip.
None of the sooties was noted with certainty at Bird Key. This is the first successful flight over open water where no shore-line is visible that has ever been recorded in any homing bird. The homing pigeons' flight over open water, even where there is a coast-line, rarely exceeds 200 km.

What makes this flight all the more surprising is the fact that the birds had a strong head wind against them all during the first day. The second day was calm, while on the last day heavy winds were again against them. Thirteen other birds, marked as shown in table 14, were taken to Galveston harbor.

TABLE 14.—*Galveston harbor release.*

Noddy:		Sooty:	
No. 1.*	Yellow, solid head.	No. 1.	Red, solid breast.
2.	Yellow, splotched head.	2.	Red, one bar left to right on breast.
3.	Yellow, left wing solid.	3.	Red, splotched breast.
4.	Yellow, right wing solid.	4.	Red, left half of breast.
5.†	Yellow, both wings solid.	5.	Red, right half of breast.
6.*	Yellow, head and right wing solid.		
7.†	Yellow, head and left wing solid.		
8.	Yellow, line from head to tail.		

*Died in passage. †Nos. 5 and 7 were mates.

The 11 birds which survived were released in Galveston harbor Saturday morning, June 4, at 5 o'clock. These birds were in a very weakened condition, owing to the fact that we had not then begun to construct our cages with individual compartments. All the birds were carried in one cage. Mr. Wilson reported that in transit the birds piled up on one another sometimes 3 and 4 deep. As their claws are extremely sharp, this resulted in much injury to the birds underneath; their feathers were torn out and the skin made raw. Furthermore, they were not eating well, for we again had not deemed it necessary to provide minnows for the full trip. When they were released all the birds flew ashore and alighted upon the sand. They were released in a light head wind. On the following day a heavy wind set in against the birds and continued all day. On June 8 Mr. Wilson left Galveston for Key West. On June 9, at 4 p.m., he saw one of the marked sooties resting upon a piece of driftwood. The red marking was plainly visible to the naked eye and still more clearly to be seen with the glasses. The bird was seen by several other people, including Mr. Greenwood of Galveston and Mr. Brown of the First National Bank of New York. The distance out from Galveston was approximately 409 statute miles. Mr. Wilson is one of the zoological collectors of the Laboratory and is thoroughly familiar with both species. He reports that with the above exception neither of the two species was seen either going to or coming from Galveston farther out than 18 miles from Bird Key (boats leaving Key West bound for Galveston pass within 4 miles of Bird Key). This attempted return of the sooty is quite remarkable in view of the fact that the direction which he had chosen was almost due east (the Mallory boats steam due east and west on these trips for a large part of the way).

Even up to June 11 we had hopes that some of these birds would return, but on that day a heavy and continuous wind set in from the south against them, which finally ended in a storm against which no bird on the open water could contend. As the Galveston birds which we did get to return on our second attempt required about 6 to 11 days (see p. 58), it is probable that the birds on this first release were overtaken by the storm before they reached Bird Key.

THE FIRST MOBILE TRIP.

On Friday, June 3, 1910, we captured 7 noddies and 7 sooties, which were sent to Key West on the *Vellela* at daybreak June 4. They were marked as shown in table 15.

TABLE 15.

Sooty:
No. 1. Orange, cross on breast.
2. Orange, one vertical line on breast.
3. Orange, one horizontal bar on breast.
4. Orange, splotched breast.
5. Orange, solid breast.
6. Orange, left half neck and breast.
7. Orange, right half neck and breast.

Noddy:
No. 1. Bright greenish yellow, cross on head.
2. Bright greenish yellow, one vertical line on head.
3. Bright greenish yellow, one horizontal bar on head.
4. Bright greenish yellow, splotched head.
5. Bright greenish yellow, solid head.
6. Bright greenish yellow, left half head and left wing.
7. Bright greenish yellow, right half head and right wing.

It was found impossible to purchase a supply of minnows and more than half the birds died before reaching Mobile. Those which reached Mobile alive were released on Thursday, June 9. The weather conditions were favorable on the 9th and 10th. On the 11th a heavy wind set in which by night had veered around to the south, becoming a veritable wind-storm. On the 12th the storm from the south still continued. All day it was cloudy and windy. After this time we gave up hopes of the return of the birds. None appeared during the time of our stay at Bird Key.

THE SECOND MOBILE TRIP.

The birds were captured May 5, 1913. They were sent to Key West by the government tug *Peoria* at 8 p. m., May 6. On May 7, they were shipped from Key West by the Mallory Steamship *Alamo,* in charge of Dr. K. S. Lashley. They were marked with green as shown in Table 16.

TABLE 16.

No. 1.	Right wing.
2.	Left wing.
3.	Both wings.
4.	Top of head.
5.	Breast.
6.	Breast and right wing.
No. 7.	Breast and left wing.
8.	Breast and top of head.
9.	Breast and both wings.
10.	Two horizontal lines across breast.
11.	Cross on breast.
12.	Two vertical lines on breast.

As the care of the birds on board the boat is probably the most essential part of a successful experiment in homing, and as it has taken us some time to learn the proper methods of handling the birds, we give Mr. Lashley's report in full. It seems worth mentioning that it was not until this trip that we were able to get all of the birds to their destination in fair condition.

NOTES OF MR. LASHLEY ON THE CARE OF THE BIRDS DURING THE MOBILE TRIP.

May 6: Arrived at Key West with birds in good condition. Wing and tail feathers a bit broken. Purchased a large fish and cut it up to feed the birds, since I was unable to get any large supply of minnows. Gave the birds salt water, with which they wet themselves badly. Placed two pieces of cut fish in water in each compartment for the birds to eat. I do not wish to use forced feeding unless necessary. If they have not taken the fish by morning I shall offer them minnows which I have obtained, using forced feeding wherever necessary.

May 7, 10 a. m.: Each bird was offered minnows. Nos. 2 and 7 each ate 2. The others had to be forcibly fed. Birds are damp and badly frayed. The strips of large fish were not eaten by any of the birds.

May 7, afternoon: More minnows were offered; 2 were forced on each bird which did not eat of its own accord. Food records were kept separately.

Left Key West May 7, 11 p. m.: Birds were loaded on top of deck house. Cage was closely hooded with canvas.

May 8, 6 a. m.: Gave birds 6 minnows each. All but Nos. 3 and 9 ate without being forced. These two ate 2 minnows each and then refused. I forced 4 more on each at 10 o'clock and left 6 to 8 minnows in each compartment. Birds are keeping themselves clean.

May 8, 4 p. m.: Birds fed again. Nos. 3 and 9 again refused and had to be forced. No. 3 is more eager to escape than the others.

May 10: Tampa was reached. Made 2 trips to Ballast Point in order to obtain minnows. Obtained only enough for one feeding. Birds ate them eagerly. On account of accident *Alamo* tied up until afternoon of May 11 for repairs.

May 12: Only a few minnows left and these not keeping very well. Obtained a large fish from the steward, but birds would not eat it; then gave them the rest of the minnows, about 15 each, exhausting the supply. This was at 11 o'clock. There was no food for them in the afternoon. For the last 3 days I have put no water in the cages. The birds come half way out of the door to eat and so keep dry. They do not show the need of water and probably get enough with the fish to satisfy them. Nos. 3 and 9 are recovering and seem to be in better condition than they were on Friday.

May 13: We reached the outer harbor of Mobile late last night and anchored. Started in at 4 a. m. to-day. Waited until we were near land before releasing the birds. At $5^h 45^m$ we passed a long island of dredged sand about 5 miles out from Mobile. I released the birds at this point. The morning was bright and warm. Sun about 20° above the horizon. Light wind from east. Ship steaming due north. Land to eastward just visible. Sand bar 500 yards to west with land a couple of miles beyond.

No. 1 released $5^h 45^m$: Feathers in good condition but damp; was frightened and flew off unprepared; alighted in water 100 yards from shore; arose instantly and flew on towards land; was attacked by laughing gulls; arose and flew away in a direction a little south of east, alighting and arising again frequently.

No. 2 released at $5^h 55^m$ a. m.: Conditions the same. By this time No. 1 had disappeared. Released No. 2 from port side with head towards land. Bird flew down from top of deck house towards water, then swerved in a direction a little south of east and flew rapidly and smoothly about 6 feet above the water.

No. 3 released immediately after No. 2: Conditions the same. It overtook No. 2 and both disappeared, still flying and holding their eastern course.

No. 4: Ran about on deck for a short time, stretching wings; then took flight to starboard and took the same course as Nos. 2 and 3.

No. 5: Drier and in better condition than the preceding birds. Ran about on deck for a minute. Took flight to westward, but immediately swerved around to east.

No. 6: Not in best condition. No. 5 did not fly until No. 6 was released and No. 6 attempted to follow him immediately without preliminary wing stretching. It struck the rail and fell to the deck, but recovered itself quickly and followed No. 5.

No. 7: On release stood on the roof of the deck house for 5 minutes, until after No. 9 took flight. Was dry and in good condition. Took flight from starboard to eastward with No. 10.

No. 8: Good condition. Took flight from port side, swerving around to east.

No. 9: In very poor condition. Damp and weak. Started to the westward, then flew to land. Made several false starts to eastward, returning to land. Was perched on a rock when I last saw it.

No. 10: In fair condition, but damp and frayed. Started west, but swerved around to east.

No. 11: In the same condition as preceding bird. Went off with it and was joined by No. 7.

No. 12: Dry and in good condition; turned eastward immediately.

None of the birds rose above the top of the deck house before taking flight. The direction finally taken by all was the same, although they were released in three groups which were, I believe, not visible to one another. No. 1 was the only one which went into the water, and this was due to some extent to the attack of the gulls. None of the others was attacked. After the preliminary movements they all flew low, not over 3 to 6 feet above the water. All were flying strongly when last seen.

Table 17 shows the number of minnows eaten during the Mobile trip.

TABLE 17.—*Number of minnows eaten on trip to Mobile.*

No. of bird.	Wed.	Thur.	Fri.		Sat.		Sun.		Mon.	Total.
			a. m.	p. m.	a. m.	p. m.	a. m.	p. m.	M.	
1	*3	*4	10	9	10	5	7	5	15	68
2	3	3	10	8	8	4	5	5	15	61
3	3	3	10	*9	0	*5	3	5	15	53
4	3	3	10	5	9	4	7	5	15	61
5	3	3	10	7	10	4	7	5	15	64
6	4	3	10	9	10	4	7	5	15	67
7	8	2	12	10	8	7	7	5	15	74
8	3	2	7	11	8	4	7	5	15	62
9	3	3	5	*3	0	*5	5	5	*15	44
10	3	3	10	3	11	4	7	5	15	61
11	10	3	10	10	10	4	8	5	15	75
12	4	3	7	9	10	4	9	5	15	66

*Forcibly fed.

BIRD KEY NOTES ON THE RETURNS FROM THE SECOND MOBILE TRIP.

On May 20 bird No. 2 returned, probably in the night of May 19, since it was observed at $7^h 30^m$ a. m. The marking was not erased in any way. The mate had deserted the nest. The marked bird was found sitting on a limb within 3 feet of the nest and was noticed near it for 3 days, usually sitting on a nearby limb. The egg and nest were not taken until the afternoon of May 23; then we saw the marked bird (a male) for the first time on the nest. The time required for return was about 7 days. This is the only bird which we ever observed returning from the trip.

The location of the nests was unfortunate. They were nearly all flat on the ground, the nesting material being placed in the grass. The grass grew rapidly and in a few days it was difficult to locate the nests. Furthermore, the rats took the eggs the moment the O's began to go for food. We replaced the eggs many, many times from nearby nests, but the rats robbed them so consistently that the O's, after a very few days, all deserted. This choice of the noddy nests was unfortunate from another side as well. Even when the nest is deserted or destroyed the occupants of the nest will often sit on limbs near the nesting place. On account of the absence of bushes near the nests of the Mobile birds, it would have been difficult to have located the birds had they returned. It must be said that on account of these difficulties we redoubled our efforts to locate the birds, sometimes sitting near the nests for 3 or 4 hours without leaving.

THE SECOND GALVESTON FLIGHT.

Twelve noddies and 12 sooties were captured on Bird Key at 2 p. m., May 15, 1913, and were left there that night. The numbers and markings of the birds are given in table 18.

TABLE 18.

Sooty:		Noddy:	
No. 1.	Red, dab on throat.	No. 13.	Red, dab on throat.
2.	Red, dab on head.	14.	Red, dab on head.
3.	Red, dab on right wing.	15.	Red, dab on right wing.
4.	Red, dab on left wing.	16.	Red, dab on left wing.
5.	Red, dab on breast.	17.	Red, dab on breast.
6.	Red, dab on both wings.	18.	Red, dab on both wings.
7.	Red, two dabs on neck.	19.	Red, two dabs on back of neck.
8.	Red, two dabs on breast.	20.	Red, two dabs on breast.
9.	Red, throat and right wing.	21.	Red, throat and right wing.
10.	Red, throat and left wing.	22.	Red, throat and left wing.
11.	Red, head and left wing.	23.	Red, head and left wing.
12.	Red, head and right wing.	24.	Red, head and right wing.

On May 16 they were taken to Key West on the *Anton Dohrn*. On May 17 the birds were put on board the Mallory freight steamer *San Marcos*. Mr. Lashley's record of the care of the birds on the trip and their behavior during release follows:

> The first food was given on May 17; 3 minnows each were given by forced feeding. From this time on the feeding was continued as shown in table 19. It will be seen that on the afternoon of the 19th no food was taken. Food was placed in the cages to see if the

birds would eat of their own accord; it was not eaten. On the whole trip only 3 birds learned to eat of their own accord. The others were fed entirely by forcing. We give the table below in order that the future investigator may know (1) that the birds may reach their destination in good condition when forced feeding has to be resorted to, and (2) because it will enable the investigator to know the number of minnows, etc., required to maintain metabolism.

Table 19.—*Food record on the Galveston trip.*

Birds.	May 18.		May 19.		May 20.		May 21.		May 22.		May 23.		May 24.		Total minnows consumed.
	a.m.	p.m.	a.m.	p.m.	a.m.	p.m.	a.m.	p.m.	a.m.	p.m.	a.m.	p.m.	a.m.	p.m.	
Sooties.															
No. 1	3	0	0	*	4	..	3	5	2	3	5	10	5	..	35
2	3	4	3	*	6	..	6	13	9	10	10	13	9	..	86
3	3	2	3	*	7	..	3	5	5	5	5	10	5	..	52
4	3	3	3	*	6	..	3	6	5	5	5	10	5	..	54
5	3	3	3	*	6	..	10	14	10	10	10	12	9	..	90
6	3	3	3	*	6	..	3	5	5	5	5	10	5	..	53
7	3	3	..	*	6	..	3	5	1	..	..	..	..	..	21
8	3	3	1	*	5	..	9	8	10	..	..	..	..	..	39
9	3	3	0	*	1	..	4	5	0	..	..	..	..	..	16
10	3	3	1	*	5	..	5	5	2	..	..	..	..	..	24
11	3	3	0	*	4	..	3	5	5	..	..	..	..	..	25
12	3	3	0	*	6	..	3	5	1	..	..	..	..	..	21
Noddies.															
No. 13	3	3	0	*	6	..	3	5	5	5	5	10	5	..	50
14	3	3	3	*	6	..	3	5	5	5	5	6	5	..	49
15	3	3	3	*	6	..	3	5	5	5	5	10	5	..	53
16	3	3	3	*	6	..	3	5	5	5	5	10	5	..	53
17	3	3	3	*	6	..	3	5	5	5	..	..	..	..	33
18	3	4	3	*	6	..	3	6	5	5	..	..	..	..	35
19	3	3	3	*	6	..	3	7	6	..	..	..	..	..	31
20	3	3	3	*	6	..	3	5	5	..	..	..	..	..	28
21	3	3	3	*	6	..	4	5	5	..	..	..	..	..	29
22	3	3	3	*	6	..	3	6	5	..	..	..	..	..	29
23	3	3	3	*	6	..	4	6	4	..	..	..	..	..	29
24	3	3	3	*	6	..	3	6	5	..	..	..	..	..	29

*Offered food, but would not eat.

The cages were kept in what had been the dining saloon of the ship (the *San Marcos* was formerly a Mallory passenger and freight boat; it had been converted entirely into a freighter). The canvas hoods of the cages were kept closed, except at feeding time, so that the birds had practically no chance to see anything which would give them their bearings. The following is a record of the releases *en route* to Galveston and at Galveston; the behavior of the birds on release follows:

May 20: Two birds released at night. Nos. 19 and 23 were selected as the best fed of the lot. No. 19 had 31 fish in all; 7 of them at 4 p. m. and 6 at 7 p. m. No. 23 had had 29 fish in all; 6 at 4 p. m. and 4 at 7 p. m. Both birds were in excellent condition, perfectly dry and clean. The tips of their wings were frayed for half an inch and the two lateral feathers of the tail. No. 23 was most active and the strongest of the noddies. It had never eaten of its own accord. No. 19 began to eat, without forcing, the day of release. The birds were released at $8^h 45^m$ ship time, and after all traces of sun had gone. The ship was headed a little north of west. The smoke was carried forward from the stack, which meant that there was a more than 10-mile breeze from the east (against the birds). The sky was slightly clouded but not hidden. The ship was 372 knots from Key West and 220 from the nearest mainland, 88° west longitude and 26° 4′ north latitude, steaming almost due west. Both birds were placed upon the roof of the after-deck house. No. 19 was frightened and flew away at once. No. 23 refused to fly, vomited up its fish, plumed itself, and settled itself down on the roof, apparently for the night. I climbed up on the roof, whereupon it took fright. Both birds started to the northward and were lost sight of immediately.

Strange to say, No. 23, after a time, came back on board the ship and was captured by one of the sailors at 9 p. m. I examined the bird and found it dry and uninjured and released it again to the northward. About an hour later it came back on board again. It was frightened off by a sailor, but returned 10 minutes later. I decided to let the bird have its way and find out how far it would follow the ship. Remained on the deck until 7 in the morning, then flew eastward, alighting in the water half a mile from the ship. At this time the ship was 500 knots from Key West.

May 21, 8 a. m.: Released 4 noddies, Nos. 20, 21, 22, 24, and 6 sooties, Nos. 7, 8, 9, 10, 11, 12. The sooties all took flight at once. No. 12 first, when released, flew due east. The others went to the northeast, flying strongly. No 11 went down into the water. The noddies showed a tendency to hang around the decks, but finally all dropped astern and alighted in the water. The birds on release were all dry. The breasts and tail feathers of the sooties were badly soiled, but not caked with excrement. The tips of their wings were broken for half an inch and the lateral feathers of the tail were broken off in most cases. The day was clear, with a light breeze from the south. The position of the ship was as follows: 520 knots from Key West, 240 knots from Galveston, latitude 27° 52′ north, longitude 90° 3′ west.

May 21, 7 p. m.: Released two noddies, Nos. 17 and 18. The sky was completely overcast. A little wind. Both went astern and settled in the water. Heavy rains set in during the night and continued steadily during May 22. This unquestionably gave the birds a much harder task to accomplish than was ever put upon a homing bird before.

May 23: Clear morning with strong wind from east. *San Marcos* lying at wharf. Small sand island half a mile to northward. Fed remaining birds and turned them loose on deck. All were dry and clean and seemed to be in good health. Fed as shown in table 19. No. 13 was released first at 5h 30m a. m. It flew down to the sand island and alighted. The others sat on the deck for some time. The sooties then took flight, all reaching the sand island. The remaining 3 noddies flew down to the water and began to wallow in it near to the ship. They then arose and began to fly, flying with some gulls. At 7 a. m. they were still fishing and flying strongly and at that time were lost sight of to the westward. The 3 noddies, Nos. 14, 15, and 16, were observed again at 12h 50m p. m., fishing from the Mallory dock. Their flights were short, not more than 800 yards. They sat on the dock a good part of the time. The birds were lost sight of soon after the above record was taken and were not seen again.

RETURNS TO BIRD KEY FROM THE SECOND GALVESTON FLIGHT.

The record of the returns of these birds to Bird Key is given below in the form of field notes. The nests were observed several times each day. Every effort was made to keep the nests in good condition, to drive out strange birds, etc. We had been especially fortunate in choosing our locality; the nests were not molested very much by rats, gulls, and other enemies of the birds.

May 25: Noddy No. 22* was noted on the nest at 5h 15m a. m. Evidently the bird had returned the afternoon of the 23d in good condition. Took nest and began habit of sitter. Mate on nearby limb. This mate had not been any too faithful.

May 25: Sooty No. 9 noted on the nest at 2h 45m p. m.; might have arrived earlier in the day, since I was at Loggerhead from 9 a. m. to 2h 45m p. m. Bird in splendid condition. Red markings showed easily and clearly. Was sitting egg eagerly.

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*Refer to Lashley's notes (p. 54) for time of release, weather conditions at time of release, distance from Bird Key, etc. The numbers of the birds given here are the same as those in Lashley's notes.

May 26: Noddy No. 20 noted at 10^h 30^m a. m.; was on limb near nest. Evidently had returned some time earlier in the morning. Poor condition. Seemed tired and worn. After a few days' rest bird began regular nesting activities.

May 27: Sooty No. 8 noted at 5^h 30^m a. m., in good condition; took nest and sat on egg.

May 27: Sooty No. 10 noted at 5^h 30^m a. m., in good condition; was sitting egg when noted.

May 27: Noddy No. 24 returned at 12^h 14^m p. m., very tired; took nest and was on nest when observed. Feathers in good condition. After a few days of rest normal nesting activities were resumed.

May 28: Sooty No. 12 found on egg at 9 a. m., in good condition; seemed quite fresh; was eagerly tending egg.

May 29: Sooty No. 11 on nest at 5 a. m., covering egg eagerly; condition good. This bird was very fierce when captured; had lost none of its fierceness; stood ground while I came up to the nest; mate not on hand. R must have come back at night, as it was not there at dark on the day before.

May 29: Sooty No. 1 noted on nest at 7^h 30^m a. m., in good condition; not sitting on egg; mate had deserted egg several days before.

May 30: Sooty No. 5 noted on nest at 11^h 35^m a. m., in good condition; sitting on egg.

June 2: Noddy No. 18 noted near nest at 8 a. m.; did not take nest; discovered by accident. The mate had been away, or rather idly sitting by, for several days. To-day and yesterday O had been on the nest more than usual. This aroused my suspicions, so I made a more thorough search. The bird seemed tired; did not fly away from limb as I approached, as rested birds always do. Possibly it did not return until to-day.

June 4: Noddy No. 14 noted near nest at 5 a. m. in fine condition; marking very clear; did not take nest at first, since nest mate was on. Yesterday I had decided that this nest had been deserted by O. I had often seen O nearby, flirting with a strange bird. Yesterday morning was actually taking food from strange bird in the nest. This morning both these birds were on and refused to let the marked bird on the nest; interesting to see if nest can be reëstablished. (R fought with the intruder for several days to get possession of the nest, but nesting relations were never resumed between R and O.)

June 7: Noddy No. 17 noted on nest at 7^h 30^m p. m. Bird probably had been back since June 5. Marking on breast had almost disappeared; hence my failure to note. This morning when I went out both birds were at the nest. This caused thorough examination, with the result that the marking was clearly recognized. Both were tending the nest. O had been very faithful all during R's absence.

The results of the second Galveston trip are put in convenient form in tables 20 and 21.

TABLE 20.

Date.	No. of birds released.	Distance from Key West (in statute miles).	Returned.
May 20, 8^h 45^m p. m.	2 (both noddies)........	418	None.
May 21, 8 a. m.....	10 (6 sooties, 4 noddies)..	585	8 (3 noddies, 5 sooties).
May 21, 7 p. m. (dark, rainy night).	2 (both noddies).......	720	2
May 23, 5^h 30^m a. m.	10 (4 noddies, 6 sooties)..	855	3 (1 noddy, 2 sooties).

The Galveston-Tortugas flight is deserving of some comment, as it shows the remarkable homing ability of these birds. It was not until this final trip that the conditions for caring for the terns approached those which are maintained for the homing pigeon. Even upon this trip the mistake was made of making the compartment too small. This tended to fray the feathers of the birds in such a way that the birds were probably somewhat hampered in their long homeward flight. That more birds did not return from Galveston harbor is not to be wondered at when we consider the number of hawks which line the Texas shores. Our birds reached there tired out and probably remained on the shore for a time to rest; they would have made easy victims for birds of prey. It is probable that the hawks are in part to blame for the poor results we obtained from the Mobile flights.*

Table 21.—*Time required for return (individual birds).*

585-mile release.	720-mile release.	855-mile release.
No. 8, 5 d. 5½ h.	No. 17, 17 d. 2 h.	No. 1, 6 d. 2 h.
No. 9, 4 d. 6 h.	No. 18, 11 d. 13 h.	No. 5, 7 d. 6 h.
No. 10, 5 d. 21 h.	....	No. 14, 11 d. 23½ h.
No. 11, 7 d. 21 h.		
No. 12, 7 d. 1 h.		
No. 20, 5 d. 2½ h.		
No. 22, 3 d. 22½ h.		
No. 24, 6 d. 4½ h.		

It would seem from all these experiments that where proper conditions are maintained the noddy and sooty can home from almost any distance up to at least 1,000 miles. Furthermore, the territory over which they take their flight apparently may be barren of any visual objects to which they previously may have established habits.

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*In future experiments we suggest that they be released not less than 50 miles from any land.

BEARING OF THE PRESENT STUDIES UPON THE GENERAL PROBLEM OF HOMING.

We shall not here attempt to summarize our results in detail, but in the present volume there are two other papers (see p. 61 and p. 87) which throw some light upon the problem of distant orientation. We shall incorporate the main results of these papers with the results obtained from the present study and trace the bearing of the whole series upon the general problem of homing.

(1) Lashley (p. 61) has shown that the problems of proximate orientation are relatively simple and straightforward. On the island of Bird Key the terns make their adjustment to the nest, mate, young, etc., on the basis largely of visual habits. Kinæsthetic habits are involved, but to a less extent. There is no evidence of any remarkable or unusual sensitivity, nor of the functioning of any hypothetical sense-organ.

(2) The present paper seems to call for a separation between proximate orientation and distant orientation. We have never in the work on the homing pigeon been able to obtain sufficient evidence to reach such a conclusion. This arises from the fact that the pigeon has always been trained over a large part of its route. Such training allows the formation of numerous visual habits; hence all orientation may be looked upon as being of the proximate kind (we do not affirm such to be the case, however). The work at Tortugas, on the other hand, has placed us squarely before the problem (to take the limiting case) of accounting for the return of an untrained bird from a distance of 800 to 1,000 miles over a body of water which apparently can not offer any basis for controlling flight direction.

NOTE.—Two suggestions looking toward a simple explanation of the homeward flight of the terns have been made: (1) that the Hatteras birds simply followed the coast-line back to Key West, from which point they could see (?) Tortugas, and further, that they followed the coast-line south rather than north by reason of the fact that the former direction led them into warmer regions, which they instinctively seek; (2) that the Galveston birds and those released *en route* were aided by a well-marked water-current which sweeps around the coast of Texas, Louisiana, Alabama, Florida, and out past Tortugas through the Straits of Florida. This main current differs in color both from the surrounding and more stationary water, and from the return current, which runs nearer the coast line. We are indebted to Dr. W. J. Humphreys for the latter suggestion. Interesting as these suggestions are, it remains to be said that the explanation offered by (1) does not bear at all upon the more difficult Galveston flight. Dr. Humphreys' suggestion (2) meets with difficulty when we remember that some of the (successful) birds were released at night and that all of the birds were out from 4 to 20 nights. Furthermore, they had to win their way through rain, haze, and cloudy weather. Nor were all the birds which returned released at Galveston. They home equally well, no matter at what point between Galveston and Tortugas they are put down. Then, too, the difference in brightness or color between the current in question and the surrounding water depends largely upon the position of the sun with respect to the observer. Apparently the birds flew steadily (sigzagging, of course, for food) from morning to night (if not through the night), and during only a part of this time would the sun have a position such that the current could offer a difference in color or in white value. Even granting the existence of such data, the question as to why the bird follows the current towards the Straits of Florida rather than in the opposite direction is pertinent. There can be no question of any permanent temperature differences among these regions during May and June, nor can there be any question of chance, when the whole group of birds is considered.

(3) Mathematical considerations show that at such distances the goal can not possibly (directly) visually stimulate the bird, even granting absolute visual acuity and complete absence of haze, etc. The vertical height to which the bird would have to fly in order to overcome the sphericity of the earth is

so great that there could be no question of direct visual stimulation offered by the goal (which in this case we may consider to be the lighthouse, 151 feet in height) at distances greater than 100 miles (probably far less than this when we consider the fact that there is a continuous haze over the water). Even at 100 miles the bird must fly to a height of 0.9 mile in order to receive the light rays reflected from the goal.

(4) We have shown that the hazardous speculation of Duchâtel, which was designed to overcome the difficulties of the visual hypothesis discussed in (3), is without foundation in fact. The investigation reported on page 87, on the limits of spectral sensitivity in birds, shows clearly that neither the chick nor the pigeon is sensitive to infra-luminous rays. Furthermore, it was shown that the retina of the chick (and incidental confirmation has been found in tests on the pigeon) is probably less efficient in responding to monochromatic light of low intensity than the retina of the human being. The single exception to this statement is to be found in the extreme red, where the retina of the chick is slightly more sensitive than man's. If these facts are considered in connection with Johnson's work, which shows that visual acuity in the chick is far less than in man, we may very well accept with caution the popular view concerning the perfection of the organ of vision in birds.

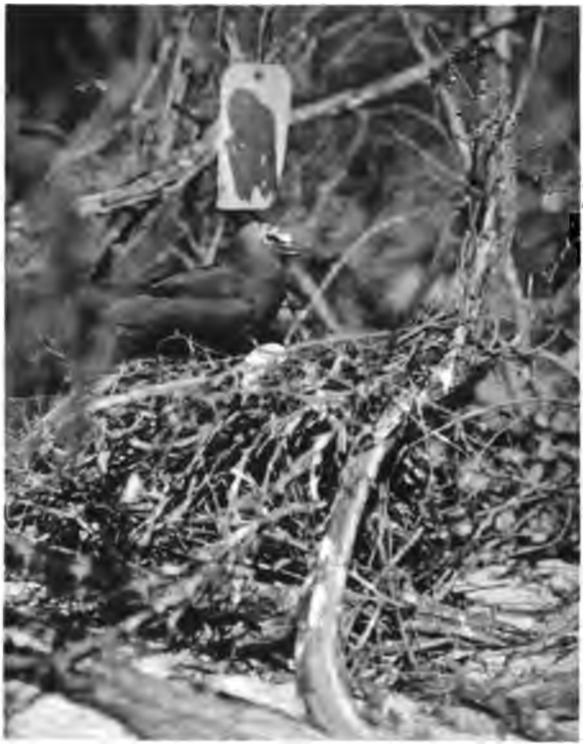
(5) Our work has shown further, in the terns at least, that there is no special Spürsinn—special tactual or olfactory mechanism situated in the nasal cavity which may function in homing.

Our contributions are admitted to be negative in character. The difficulty of explaining homing by current theories is seen to be great, but, while admitting this, we do not suggest the assumption of some new and mysterious sense. The task of explaining distant orientation is an experimental one, which must yield positive results as soon as proper methods are at hand. Two lines of investigation offer hopeful results:

(*a*) The rearing of homing pigeons in a côte which is covered by a tent sufficiently large to offer the birds wing practice and to make proximate adjustments to their côte. Birds reared under such conditions may be sent out for a test of the possibility of homing in an untrained animal. After shipping the birds the tent which covers the côte could be removed. If they returned to the neighborhood the visual stimulus offered by the côte would arouse the old habit of entering it, etc.

(*b*) The same possibility is offered on a smaller scale by a slightly similar method. We could rear the birds in a wire-covered yard attached to a côte; then, as was done by Hachet-Souplet with the birds living in the traveling côtes (an experiment which certainly ought to be confirmed), we could tether individual birds to the top of the côte by cords which would permit a view *only of the neighborhood immediately surrounding the côte.* These birds would next be sent into a region which could not have stimulated their vision previously. Again, if the birds effected a return to the neighborhood of the côte, they would resume their old habits.

With these experiments upon homing, work upon the sensory equipment of the homing pigeon should be carried on. It is just possible that these animals possess on certain parts of the body (eye-lids, ear covering, oral cavity, etc.) sensitive tactual and thermal mechanisms which may assist them in reacting to slight differences in pressure, temperature, and humidity of air columns.



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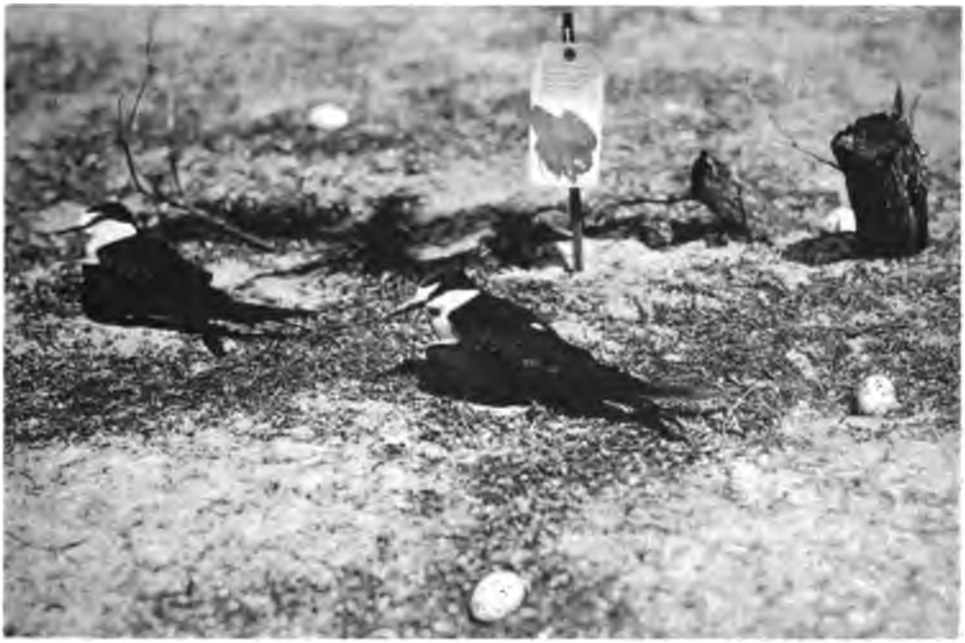

2

METHOD OF MARKING NEST AND BIRD FOR HOMING.

Fig. 1. Noddy nest tagged. Four horizontal bars are painted in oil across the bird's head.

Fig. 2. Sooty nest tagged. Large daub of oil paint is placed on the bird's white neck.

NOTES ON THE NESTING ACTIVITIES OF THE NODDY AND SOOTY TERNS.

BY K. S. LASHLEY.

ORIENTATION IN THE NEST LOCALITY.

In the report of his extensive studies of the activities of the noddy and sooty terns* Watson raises the question of the method by which the birds recognize their nests and young and records the results of a few experiments bearing upon the problem. The terns breed in great numbers upon Bird Key, an island in the Tortugas group somewhat less than 5 acres in area. Their nests, of which there were more than 10,000 in 1908, are in may cases closely crowded together, as many as 30 sooty nests being found in an area of 100 square feet, and the nests and eggs are almost indistinguishable to the human observer. Indeed, the island suggests a city of 10,000 houses, all much alike, unnumbered and set down at random, without streets or definite landmarks. The birds choose their own nests, without error, from among hundreds of similar ones, and under normal conditions never show the slightest hesitation in making their choice.

In testing the sensory factors involved in nest recognition, Watson found that he might change the appearance of the nest and egg without disturbing the birds in the least. Very great changes in the appearance of objects near the nest did not alter the quickness and accuracy of orientation. When, however, the slightest alteration was made in the horizontal position of the nest, when it was moved only a few inches to one side, the birds were much confused, refused to occupy the nest in its new position, and reacted positively to the original nest site even when no trace of the original nest remained. Many observations of such behavior led Watson to conclude:

> In the case of both the noddy and the sooty, the nest locality is the important factor, the nest itself being reacted to by virtue of its location within this locality. Since environment can be greatly changed without altering the bird's accurate adjustment to the nest, it is evident that if the adjustment is made in terms of visual data, the visual environment which serves as the stimulus must be complex and have a wide extension. I am not prepared to admit, from the above experiments, that adjustment takes place in terms of vision alone.

In view of the remarkable ability of the terns to return to their nests from great distances the problem of the sensory factors involved in their recognition of the nest locality and orientation in the neighborhood of Bird Key becomes of considerable importance as offering a possible aid to the understanding of more distant orientation.

At the suggestion of Professor Watson I attempted to gain further evidence upon the problem of proximate orientation in the terns during a six weeks' residence on Bird Key. The work has not furnished any clue to the mechanism of distant orientation, but the details of the birds' behavior in finding and recognizing their nests seem worth recording as exemplifying the extremely complicated habit-systems which wild animals may develop under a normal environment, and, also, as showing that, whatever the mechanism of distant orientation may be, proximate orientation is readily explainable in terms of visual and kinæsthetic habits.

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*John B. Watson. The Behavior of the Noddy and Sooty Terns. Papers from the Tortugas Laboratory of the Carnegie Institution of Washington, Publication 103, 1908. In this is included a general description of the activities of the terns during the nesting season. The reader is referred to the paper for figures of the birds at different ages and for a more complete description of the behavior of the birds at different times during the nesting season than is given here.

I wish to express my indebtedness to Professor Watson for much helpful suggestion and coöperation in the work, and to Dr. Alfred G. Mayer, of the Carnegie Institution of Washington, for his kindness in placing the facilities of the Marine Biological Laboratory at my disposal.

Plate 7, figs. 1 and 2, show roughly the character of the nesting areas of the sooties and noddies. Detailed descriptions of the nests and eggs have been given by previous writers, and the following brief notes are included only for the sake of a clearer presentation of the experimental control of orientation.

The nest of the sooty consists usually of a shallow depression in the sand, of about the depth and diameter of a large saucer. The birds hollow it out by a sort of wallowing movement, turning around and around and pushing the sand away with their breasts. In this depression a single egg is laid. Rarely two eggs are found in a single nest, but whether both are laid by a single bird, or one is stolen from a neighboring nest, is uncertain. In 1913 the greater number of sooty nests were made on the western end of the island. Their position and relative number are indicated by the stippling in figure 2. The nests of the noddies are loose masses of sticks piled among the branches of the low shrubs which cover the greater part of the island. They are frequently lined with bits of coral and shells, and, like the nests of the sooties, rarely contain more than a single egg.

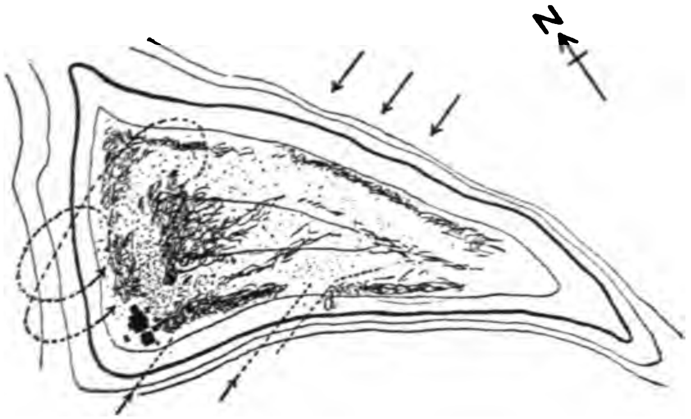

FIG. 2.—Diagram of Bird Key. Buildings in black at the left. The chief nesting areas are represented by stippling. Solid arrows represent direction of prevailing winds. Dotted lines show chief paths followed by birds in approaching the island.

The key upon which the nests are built is roughly triangular, about 500 yards in length and half as broad. Its principal features are shown in figure 2. Its greatest elevation is not more than 6 feet. The key was formerly overgrown thickly with bay cedars, but the greater number of these were killed by the hurricane of 1910 and only a few living cedars remain, for the most part near the center and western end of the key. These grow to a height of 5 feet and make many irregularities in the profile of the key which are probably important as landmarks for the birds. Where the bay cedars have been washed out the sand is covered by low fleshy herbs resembling the common tumble-weed. At the beginning of the nesting season large numbers of these weeds were torn up and piled along the beach to give the sooties nesting space in the center of the island.

At the western end of the island are some buildings, the warden's house and the old detention hospital, which are the most conspicuous objects upon the island. The group of buildings is about 50 feet in length and has a maximum height of 15 feet. Three cocoanut palms (marked x in figure 2) grow near the buildings. The buildings, the palms, the clumps of bay cedars, and the piles of brush along the beach present extremely complex visual stimuli to the birds coming home from sea. Even at the most isolated nests the environment presents a countless number of possible visual stimuli and it is never practicable to control more than a very few of the stimuli which may be potent factors in the birds' orientation. Long-continued study of a single nest is prevented by the fact that the birds soon become hopelessly confused by the changing conditions of the experiment and cease to react definitely to the nest or nest environment. The situation at every nest presents a distinct problem and in no case has it been possible to reconstruct the entire process of orientation from the data obtained at a single nest. The relation between particular stimuli and the orientation of different birds has been determined, and a combination of the results of observations at many nests gives a fairly complete picture of the mechanism of orientation in the immediate neighborhood of the keys. The experiments recorded in the following pages are typical of a large number carried out at other nests and will serve to illustrate the chief phases in the recognition of the nest and nest site.

EXPERIMENTS WITH SOOTIES.

RECOGNITION OF THE NEST SITE.

The sooties become accustomed to the experimenter's presence very quickly and often become so tame as to interfere seriously with the experiments, refusing to be driven more than a few feet from the nest. After they have been disturbed a few times their return to the nest is very prompt. The accompanying table gives the time elapsing from the moment when the brooding sooty was driven from the nest until it had again covered the egg. The time given is based upon the average of 6 birds during 5 successive trials at intervals of 5 minutes. The average time which a tame sooty requires to rise from the nest, fly 15 or 20 yards and return, is 12 seconds. This is not appreciably changed by the substitution of a strange egg for the one in the nest, or by the filling in or remodeling of the nest by the experimenter, so long as the egg remains in nearly its original position. A very slight change in the lateral position of the egg, however, causes a very great increase in the time required by the bird to return to the nest and begin to brood the egg. In adjusting to such changes the sooties show a very accu-

Trial.	Time (seconds).
No. 1	56
2	25
3	30
4	18
5	12

rate localization of the original position of the nest, even when all traces of it have been completely obliterated. The following notes give a description of a typical instance of adjustment to a lateral displacement of the egg.

EXPERIMENT 1.

10^h 50^m a. m. I drove a sooty from her nest, obliterated the nest, and made a new one with a noddy egg in the same place. In 1 minute the bird returned and in 2 minutes covered the egg, after driving away two trespassers.

10^h 53^m. I obliterated the old nest and made a new one, 1 foot south of the first position. The bird alighted at the old nest and turned around as if to adjust the egg. She then caught sight of the egg in its new position and went over to the new nest, then returned to the old one. She then made 4 more trips back and forth between the new nest and the original nest site, and finally settled down at the latter, hollowing out the sand to form a shallow nest. After a minute she went to the egg, adjusted it, and settled down on it. Another sooty attacked her and she drew back from the egg without defending it, looking back to the old nest site. She next went to the old nest, then back to the egg, which she covered for 30 seconds. After one more trip to the old nest she seemed reconciled to the egg in the new position. The total time required for this readjustment was 10 minutes.

11^h 5^m. I drove her away again. She returned in 1 minute, alighted between the first nest position and the new one, went first to the egg, then to the old nest site, then back to brood the egg. Two minutes later she paid a brief visit to the old nest.

11^h 10^m. Driven away again, the bird alighted near the old nest site and ran directly to the egg. After 30 seconds she visited the old nest site, and again after 2 minutes. She was driven away 6 times during the next half hour and at the end of this time showed an almost perfect adjustment to the changed conditions, returning to the egg in 15 seconds. The egg was then returned to its original position. The bird accepted it at once and paid not the slightest attention to the new nest which she had just been occupying.

In this case the substitution of noddy egg and artificial nest for the original egg and nest did not affect the bird's reaction in the least.

EXPERIMENT 2.

In another case the egg was taken from a nest, a piece of black cloth 3 feet square was spread over the nest, and the egg was replaced on top of the cloth. The bird alighted in a few seconds and walked immediately to the edge of the cloth. It showed a good bit of hesitation in stepping on the cloth, and walked around it, looking at the egg for many seconds. In less than a minute, however, it ventured upon the cloth, seemed to lose all fear immediately, ran to the egg and covered it contentedly. The total time required for adjustment to the new situation was less than a minute.

Other instances of similar indifference to the appearance of the nest and egg are recorded in later experiments and make it clear that, except under unusual conditions, the individual characters of the nest and egg do not play any important part in orientation. The birds react positively to any nest at the chosen site. In contrast to this the birds are almost always very greatly disturbed by a lateral displacement of the nest of only a few inches and react to the original nest site much as did the bird described in experiment 1. The time required for readjustment to such slight changes varies greatly with different birds, even under quite similar conditions.

EXPERIMENT 3.

The same birds whose average time of adjustment to disturbance is given on page 63 were used for a comparison of the times of adjustment to a change in the position of the nest. The nests were similarly located in open, rather thickly populated areas, but so far apart that no two of the birds under observation were disturbed at the same time. In each case the nest was obliterated, a new nest was constructed 1 foot from the old nest site in the direction most free from other nests, and the egg was placed in this artificial nest. The birds were allowed to find the new nest and settle down quietly over the egg each time before being frightened away again. Table 22 shows the time required by each bird to readjust to the new situation. The birds were driven away at intervals of 5 or more minutes.

TABLE 22.

No. of trial.	Time in seconds.					
	Bird No. 1.	Bird No. 2.	Bird No. 3.	Bird No. 4.	Bird No. 5.	Bird No. 6.
1	240	480	300	(*)	30	100
2	15	60	270	...	20	100
3	120	240	30	...	90	50
4	150	120	40	...	(†)	50
5	15	65	55	...	...	40
6	50	75	30	...	...	20
7	15	300	36	...	...	30
8	10	90	...	...	...	50
9	10	30	...	...	...	40
10	15	30	...	...	...	...

*Did not find egg in half an hour. †Undisturbed by change.

In each case but one the birds were greatly confused by the change in the position of the nest and all showed a tendency to settle down at the original nest site. As it was clear that the nest itself was not the stimulus to the localization of this area, an attempt was made to control the immediate surroundings of the nest. The following experiments with objects near the nest give some insight into the mechanism of nest recognition:

EXPERIMENT 4.

In making their nests the sooties avoid the beach, very rarely going beyond the fringe of bushes which marks the highest tide level. A few nests were made, however, at some distance from the bushes upon the sloping sand above high-tide mark. One of these on the western shore, well removed from any other nest, was obliterated and replaced by two artificial nests, one 6 inches to the east, the other 6 inches to the west of the original site. The egg from the original nest, which was rather light in color, was placed in the western nest and another, marked with dark blotches, in the eastern one. The sand sloped from east to west at about 15 degrees.

Two minutes after these adjustments were made the sooty returned and, after inspecting both nests, chose the strange egg in the eastern one ($7^h 20^m$ a. m.). Half a minute later she got up, went over to the western nest, and covered it. Her mate came and examined the eastern nest. The first bird, attracted by his movements, went back to this nest and settled down there. Her mate then flew away. She soon became dissatisfied with the eastern nest and made several trips back and forth between the two. The visual stimulus of the unoccupied nest seemed to furnish a stronger impulse than the tactual stimulus of the nest occupied. At $7^h 25^m$ a. m. the bird stood for some time between the two nests, looking first at one, then at the other, and finally chose the eastern one. She was driven away, returned, and took the eastern nest. Half an hour later she was driven away again; she returned, again took the eastern nest, and paid no further attention to the other.

The two nests were then obliterated and replaced by two others at the same distance from the original site, but now north and south of it. The bird returned and chose the southern nest, paying no attention to the other. Control tests showed that in this case the position of the observer did not influence the choice of the nest.

One egg was then placed in the original position, the other in a new nest 3 inches to the eastward of this. The bird returned and chose the western nest, but soon left it for the other. She was driven off five times and each time returned and took the eastern nest. As she always approached from the southeast it is probable that the direction of approach determined the choice.

The western nest and egg were next moved 11 inches to the eastward, 8 inches farther from the original nest site than the former eastern nest, which was left undisturbed. The bird returned and took the new nest. The western nest was again shifted to the eastward. The bird returned and again took the eastern nest. By shifting the two nests alternately it was possible to move them 4 feet to the eastward without confusing the bird. Each time she chose the eastern nest in preference to the former eastern one which she had just occupied. But when the nests were brought near the bushes the bird began to show signs of dissatisfaction, finally returned to the original nest site, and settled down there. After a time she got up and went back to the two nests. This time she covered the western one. The nests were then shifted, a foot at a time, to the westward, the bird each time choosing the western one, until they were near the water, 4 feet west of the original nest site. Here the bird again became dissatisfied and returned to her old nest. The eggs were finally placed 8 inches east of their first position and left for half an hour. At the end of this time the bird had rolled one of them to the original nest site and was brooding it there.

In approaching the nest the bird always flew along the shore skirting the fringe of bushes, then alighted about 6 feet southeast of the nest and walked directly to it. At various times during the experiment she started from the alighting place straight toward the original nest site, but turned aside to the new nests before reaching the old position. The movements of her head indicated that she took her bearings from some object to the northward. What that was I could not discover.

It was found here that recognition of a nest is to some extent dependent upon the relative positions of the nest and other objects in the neighborhood, in this case an artificial nest. Other factors not brought out by the experiment seem, however, to play a still more important part in orientation. The constant alighting place and path to the nest furnish a clue to other factors in orientation which appear more strikingly in other experiments.

EXPERIMENT 5.

A nest in an open space (at *a* in figure 1, plate 7) near a short stake (*f*) was obliterated and replaced by two nests a foot apart. The bird chose the northern egg. Both eggs were moved a foot to the northward. The bird alighted and chose the northern egg without hesitation. Her mate came and covered the southern one. Both were driven off. The first returned and alighted at a place 4 feet to the eastward (*g*), then walked for 3 feet straight toward the original position of the nest. When still a foot away she seemed to catch sight of the eggs in the new position, turned sharply from her course, and went straight to the northern egg (*d*). She soon became dissatisfied, went back to her alighting place (*g*), and returned to the northern nest, but this time directly. She then went to the southern nest (*b*), returned to the northern, and covered the egg. Her mate came back and again took the southern nest.

Both nests were again moved, with the stake, 2 feet to the northward. The first bird alighted as usual near the bushes (*g*), walked to the original nest site (*a*), looked about, and went directly to the new southern nest (*c*). Her mate came and walked about the old nest site. She got up and went to him, then returned to the nest.

The stake was then moved back to its first position (*a*), the nests being left undisturbed in the northern position. The first bird came to her alighting place and started directly toward the new site, then seemed to catch sight of the stake and turned toward it, then back to the alighting place, toward the stake, back again to the alighting place, again toward the stake, then to another nest, where she seemed to get her bearings, toward the new nest, toward the alighting place, then finally to the new nest. The path followed is indicated in figure 3, and shows clearly the struggle between the motives offered by the sight of the stake and that of the egg.

The egg and stake were next placed 2 feet south of their original position (at *h*, in figure 1, plate 7). The bird returned to her alighting place (*g*), looked about, and went straight to the new nest. The egg and stake were then moved to a position near the alighting place (*e* in figure 1, plate 7). The bird alighted 2 feet north of the stake, went to it, and covered the egg without hesitation.

The stake and egg were moved 2 feet to the westward (*f*) and another egg was placed where they had just been (*e*). The bird returned to her alighting place, examined the egg and stake (*f*), then covered the egg in the former position (*e*). She was driven off and returned to her alighting place immediately. Another bird alighted near the unmarked nest (*e*) and disputed her possession of it, so she went to the egg by the stake and covered it. A moment later she got up and went back to the unmarked nest. The strange bird made way for her and she covered the egg there. This is the position in which she is shown in plate 7. It is in the direct line between the alighting place and the original site (*a*). The egg and stake were next placed between this position and the original nest site. The bird continued to occupy the unmarked nest. The egg and stake were returned to their original position, but the bird did not again take them.

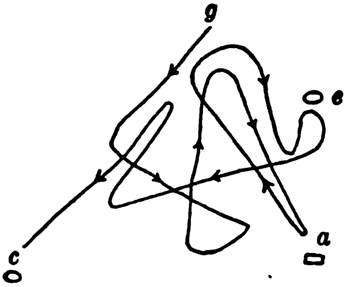

FIG. 3.—The path followed by the sooty in experiment 5 when the egg (*c*) was moved away from the stake (*a*). The reaction to the 4 chief visual stimuli of the region is shown.

This series of observations offers several interesting points:

(1) In comparison with the sooties in crowded localities, the bird under observation showed a remarkable plasticity. Attempts to duplicate the experiment in crowded districts failed completely.

(2) The constancy of the place at which the bird alighted is very striking. How this place was recognized could not be determined, but it was near an open place in the bushes which offered many more visual criteria than did the immediate surroundings of the nest. The certainty with which the direction was taken from this position to the nest is also unexplained. It was to a certain extent independent of the appearance of the immediate vicinity of the nest. The question of orientation from the alighting place will be taken up later.

(3) The relative force of the egg and stake in determining behavior gives some insight into the bird's habits with respect to the nest environment. The stake had been planted 2 weeks before to mark the site of another nest, at that time destroyed. In 2 weeks it came to occupy an important place in the bird's recognition of her nest, perhaps taking the place of the obliterated nest in her system of habits. That it was not the fundamental factor in locating the nest is shown by the fact that after a few failures to reach the nest by going to the stake the bird paid little further attention to the latter.

EXPERIMENT 6.

A nest in a rather crowded area was chosen for this experiment. It was 8 inches north of a stake which had been planted a week before to mark another nest, and near the center of a triangle (figure 4), the northern side of which was formed by a line of very dense weeds (*c*), the western by a very dense clump of weeds (*f*) and the stem of a palm leaf (*d*), the southern side (*a*–*g*) being open. The stake shown in figure 4, at the right of the nest (*b*), was originally at *h*. I drove the bird from the nest—she circled above the island and came back immediately, alighted 6 feet to the eastward of the nest, and walked almost straight to it (along the line *a*–*b* in the figure). This was repeated twice, her path in returning being each time the same.

The stake at *h* was by far the most conspicuous object near the nest, and to test its effect upon the bird's reaction I moved it from its position south of the nest to an equal distance north of the nest. I also constructed a new nest, north of the stake at the position marked *c*. The relation between this nest and the stake was now the same as the relation of the nest at *b* and the stake had been before the change. The bird's own egg was placed in the nest (*c*) and a strange egg was placed in *b*. The bird returned by the path from *a* and took its own nest at *b* after some hesitation. The change in the position of the stake was a disturbing factor, but was not sufficient to determine the choice of nests.

The line of weeds forming the northern boundary of the triangle was next moved a foot to the northward. The bird returned by its customary path without the slightest hesitation. This landmark played no part whatever in orientation.

The weeds were returned to their original position and the objects forming the western border of the triangle were moved a foot to the northward. This brought the clump of weeds and palm leaf, originally at *g* and *f*, to the position shown in the figure. The bird alighted far to the south and passing around between *h* and *e* took the northern nest at *c* and settled down quietly. She was driven away and the palm leaf was returned to its original position, *f*. The bird returned and occupied the northern nest, *c*, for 5 minutes. She was again driven away and the clump of weeds was returned to its original position, *g*. The bird returned and took the southern nest, *b*, without hestitation. The leaf and weeds were moved back to *d* and *f*. The bird chose the northern site; they were returned to the southern position, the bird returned to the northern nest, adjusted the egg, got up, walked to the southern nest, and covered the egg there.

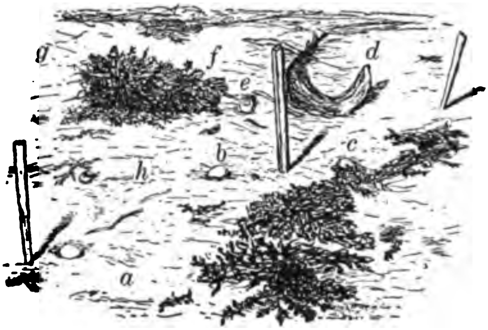

FIG. 4.—Environment of the nest described in experiment 6.

The weeds were moved northward to *f*, the leaf was not disturbed. The bird chose the southern nest. The leaf was moved to the northward. The bird chose the northern nest. Leaf and weeds were moved to the southern position; the bird came to the northern nest, hesitated for 30 seconds, then chose the southern nest. This shift was repeated many times until it was quite certain that the bird always took the same position with respect to the two objects. Finally they were removed entirely. The bird showed signs of confusion, occupied the two nests alternately for several minutes, and finally settled down in the southern nest.

The weeds to the northward were cleared away and the nest, *b*, was moved 18 inches to the northward of *c*, to a position at the extreme right of the figure. The leaf and weeds were likewise shifted to the northward, so that the original relations of the nest and two objects were now duplicated, nearly 3 feet from the original position. The bird returned and covered the southern egg at *c*; 3 minutes later she got up, went to the new nest, adjusted the egg, and covered it. I watched her for half an hour longer, during which time she remained contentedly on the nest; 4 hours later her mate had returned and taken the southern nest, which he occupied during the whole of the following day.

From this rather long account it is clear that the final orientation was determined wholly by the visual stimulus of two objects in the neighborhood of the nest. Neither the palm leaf nor the clump of weeds alone was sufficient to determine the choice of the nest, but both together called forth a definite reaction, regardless of all other objects in the vicinity.

Watson found that considerable changes could be made in the vertical position of the nest without affecting the bird's reaction in the slightest. His experiments have been repeated, but always with negative results. The following notes illustrate the type of reaction obtained:

EXPERIMENT 7.

A nest near that described in experiment 5 was placed in a pan of sand, 1 foot square and 2 inches deep, so that it was raised 2 inches above its former level. The owner of the nest always alighted 6 feet to the eastward and walked by a somewhat zigzag path to the nest. When the pan of sand was first put in place she approached, walked around it, and inspected it carefully. She next stopped, peered about in all directions, then stepped up to the higher level. She did not cover the egg, but walked about in the pan and finally backed over the edge and fell out. She spent some time standing near the pan, then stepped up on it again, and after 8 minutes covered the egg. Half an hour later she was driven away. She returned at once, spent 2 minutes in preening her feathers, then stepped up into the pan, and covered the egg immediately.

The pan was next raised to a height of 6 inches from the ground. The bird returned to her alighting place, walked toward the pan, hesitated, walked around it several times, but made no attempt in half an hour to get upon it. With the pan in this position she could not see the egg from the ground. The pan was then lowered to a height of 4 inches. The bird came from her alighting place to the pan, climbed into it with difficulty, putting one foot in it and fluttering up, and covered the egg in 2 minutes. The nest was left in this position until the following day, when the experiment was resumed. The bird was then driven off several times and each time returned to her usual alighting place, walked to the edge of the pan, then fluttered up to the egg. The nest was raised to 5 inches and was taken immediately. It was next raised a foot from the ground. The bird walked around it for 5 minutes before flying up and covering the egg. It was left in this position for an hour and was then raised to a height of 2 feet. The bird returned to her alighting place, walked to the foot of the post supporting the nest, and seemed very much puzzled by the new condition. She walked round and round the post, looking up at the nest, but in 10 minutes made no attempt to fly up to the pan. The pan was lowered to 6 inches and was occupied immediately.

The pan and its support were moved 3 feet to the westward and fixed at the same height. The bird came to the former nest site and wandered about for 10 minutes, but did not seem to see the nest in the new position. The nest was next moved 6 feet to the eastward of its original position and fixed at the bird's alighting place. The bird came to the ground beside the nest and fluttered up and covered the egg immediately without a sign of dissatisfaction. The pan was returned to its first position and fixed at a height of 6 inches. It was accepted at once.

Two days later the same bird was upon the nest. The egg had hatched in the meantime. The pan was raised to the top of a post 2 feet above the ground. The bird walked around the post for half an hour without seeming to look up at all. She then flew away and was not seen for the remainder of the day. The next day she was again in the nest. When driven off she returned and alighted directly upon the nest.

The pan was raised to a height of 5 feet. The bird came to the ground and walked around under the pan for several minutes, looking up. Then came the most interesting part of her entire series of reactions. She flew up to a height of 2 feet and went through the motions of alighting, just as though the pan were still at this height, then dropped back to the ground. She repeated this five times in exactly the same way, then walked about for a few minutes, looking up, and finally flew up to the pan and covered the nestling. She was frightened away again, returned to the ground, and flew up to the pan immediately.

This experiment brings out three facts quite clearly. First, adjustment to changes in the height of the nest is not made any more readily than to changes in the horizontal position. Second, shifting the nest along the pathway toward the alighting place disturbs the birds less than a change in the position of the nest in any other direction. Third, there is strong tendency to replace visual motor reactions by habits based upon kinæsthesia, resulting in reactions like those shown by the rat in the adjustable maze.

Clearly, in all these experiments the birds were influenced to some extent in the recognition of their nests by visual objects in the immediate neighborhood. Such objects were other nests, débris which had been in place since the nest was made, and objects recently added to the situation. It appears that long familiar objects influence orientation more than those added after the laying of the egg. The birds pay more attention to the nests of others than to any other class of objects.

In the case of some other nests, particularly those in crowded areas, I could find nothing in the immediate neighborhood of the nest which seemed to influence the birds' orientation. At one time a nest was shifted 1 foot from its original position and practically every object within a radius of 3 feet was moved for the same distance in the same direction. The sand in this area was smoothed out to change its appearance. Thus the original environment was duplicated with 1 foot lateral displacement. The bird came back to the position of the orignal nest, now completely obliterated, and gave nearly the same set of reactions as that of the bird described in experiment 1. In this case the recognition of the nest locality was upon the basis of some other stimulus than that provided by the immediate environment. The same was in part true of the nests described in experiments 4 and 5.

THE ALIGHTING PLACE.

The clue to the method of orientation in such cases is given by the behavior of the bird described in experiment 5 in passing from her alighting place to the nest. It seemed that this bird took its direction from some objects at the alighting place and depended upon this place for re-orientation when confused by changes in the position of the nest. The following observations bring out the importance of the alighting place and the path from this to the nest.

Experiment 8.

At the edge of the beach two piles of brush were thrown together in such a way as to leave a small over-arched passage extending half way through between the piles and opening on the beach to the westward (z, figure 5). A pair of sooties had their nest at the inner end of this passage. The bird studied alighted always at the southern end of the brush pile, walked around the southwestern corner, where there was another nest (x), and then followed the western side of the pile to the opening of the nest. The path was complicated by a dead bay-cedar branch (y), which projected from the face of the pile and forced the bird to stoop and turn out to the left. The bird was seen to follow this path accurately in five successive trips to the nest. I broke off the branch and removed it, leaving a clear path from x to z. On the next two trips to the nest, *the bird went through exactly the same movements of stooping and turning out which had been required by the presence of the dead branch.*

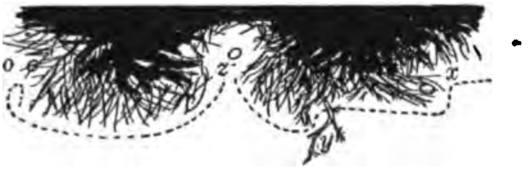

FIG. 5.—Nest environment described in experiment 8. z, nest of bird studied; x and o, other nests; y, branch of bay-cedar bush.

I moved the egg out from under the brush to a point a foot west of its original position. The bird returned immediately and went to the former position of the nest. She was disturbed by the absence of the egg, came out slowly, and returned to the southwest corner of the brush pile. She looked at the nest there, then turned and ran quickly along her usual path to her own nest. This was repeated four times. The bird's movements in going from the nest site to the corner of the brush pile had every appearance of hesitation and uncertainty, a marked contrast to her behavior after she reached the point from which the neighboring nest was visible. The sight of this nest seemed in every case to furnish the basis for orientation, for the bird always hastened back to her own nest after looking at the neighboring one. After 15 minutes she found the egg in its new position and soon covered it, to all appearances satisfied; 5 minutes later she was driven away, returned to the southern end of the brush pile, and walked to the old nest site by the customary path. She settled down in this position for a few minutes, then became dissatisfied, went over to the egg, adjusted it, and covered it.

The path from *x* to *z* was then blocked by piling brush at *y*. The bird alighted near the nest at *x*, started along the path, came to the pile of brush, and seemed to be completely lost. She wandered about for a long time and finally came to the nest (*o*) at the other end of the brush pile. She crawled into the brush and inspected this nest, then turned and scurried around to her own nest at *z* as fast as she could run. The nest at *o*, like that at *x*, served as a landmark.

Under normal conditions a nest near the alighting place furnished the bird a clue to the direction of its own nest and the path to the latter was followed almost wholly by a series of kinæsthetic-motor habits. The bird was able to re-orient from other visual stimuli when the usual method was prevented.

Experiment 9.

An isolated nest upon the beach, just at the foot of a steep sand bank covered with dead bay-cedar bushes, was chosen for observation. The environment of the nest is shown roughly in figure 6. The nest was at the position marked *d*. The brooding bird was driven off several times and her return noted. She never alighted upon the beach, but always upon the top of the bank, among other nests, at a distance of more than 8 feet from her own (at *a* or *b*). From this point she walked to her nest, following a winding path about 12 feet in length. This path led through a clump of weeds, straight down the face of the bank, around a dead bay-cedar bush, and along the foot of the bank for 4 feet to the nest. Along the path were five other nests, which were always avoided carefully. These nests were on the face of the bank; there were no other nests at its foot.

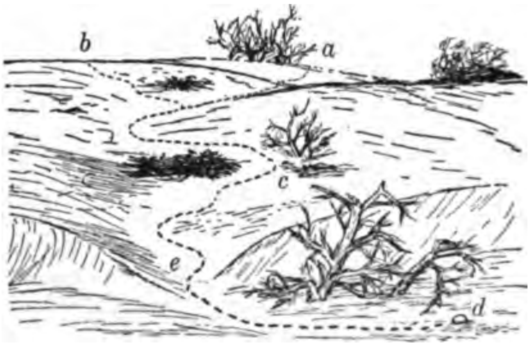

Fig. 6.—Nest at the foot of a sand bank, with the path from the alighting place shown by the dotted line.

Moving the nest along the foot of the bank for a distance of 2 feet in either direction did not seem to affect the bird's behavior in the least. A piece of canvas was placed against the face of the bank so as to cover the bird's path from the top to the foot. The canvas was nowhere nearer than 5 feet to the nest and did not cover the bird's alighting place at the top of the bank. The bird returned, seemed frightened, but in 5 minutes alighted and walked upon the canvas. She started down the bank in the right direction, but became confused as soon as she got upon the canvas, and returned to her usual alighting place. She made several more false starts, became accustomed to the canvas, and walked upon it without hesitation, but never walked the full distance to the foot of the bank. She went a short distance to one side of the canvas and reached one of the nests bordering her path (*c*). She looked at this for a moment, and then turned and ran rapidly in the direction of her

own nest, but was again interrupted by the canvas. After a great number of failures she finally reached the foot of the bank, seemingly by chance, half an hour after the canvas was placed in position, and from this place she followed her customary path to the nest. An hour later she was driven from the nest (she probably made many trips to and from it during this interval). She returned to her original alighting place at the top of the bank and flew from it across the canvas to the foot of the bank, then walked to the nest.

In this case the alighting place was far from the nest. Blocking the path between the alighting place and the nest was sufficient to destroy orientation. The immediate neighborhood of the nest was reached by chance, but was recognized at once. Readjustment to the changes in the path followed very quickly.

From many observations I am convinced that practically every sooty has a special alighting place and path which is invariably followed in the return to the nest under normal conditions. In some cases the path seems unaccountably complicated. Figure 7 shows the path followed by one bird in 10 successive trips to the nest. It passed its own nest, then around a large clump of weeds, back past its own nest at *b* to inspect the nest at *c*, and only then occupied its own nest.

In many cases it is evident that after orientation is gained the path to the nest is determined largely by motor habits irrespective of the immediate visual stimuli. Little direct evidence upon the recognition of the alighting place has been gained, and the attempt to trace back orientation beyond this point must be postponed until data from experiments with noddies has been presented.

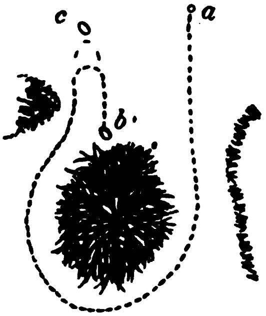

Fig. 7.—Complicated path from the alighting place (*a*) to the nest (*b*).

EXPERIMENTS WITH NODDIES.

THE NEST AND PERCH.

As in the case of the sooties, Watson found that the noddies locate their nests readily when the appearance of the surroundings has been completely altered and that the substitution of an artificial nest and egg for the originals does not disturb the birds in the least. He found also that very slight changes in the position of the nest confuse the noddies and that after such changes the birds still react positively to the old nest site. The nests of the noddies are always built upon the bay cedars and any great change in the appearance of the nest and environment involves not only a great deal of labor but also the destruction of many other nests. For this reason no great number of experiments upon the nest recognition of the noddies were carried out. Such experiments as the following, together with a large number of observations upon the flight of the birds to their nests, give, however, a fairly complete picture of the mechanism of orientation.

Experiment 10.

A pair of noddies had built their nest in a dead cedar bush near the smaller of the palm trees shown in plate 7, figure 2. When both birds were at the nest, one or the other was always to be seen perched on the middle of a low leaf of the palm. One of the birds is shown in figure 2, *c*. The nest was torn from its position and fastened on top

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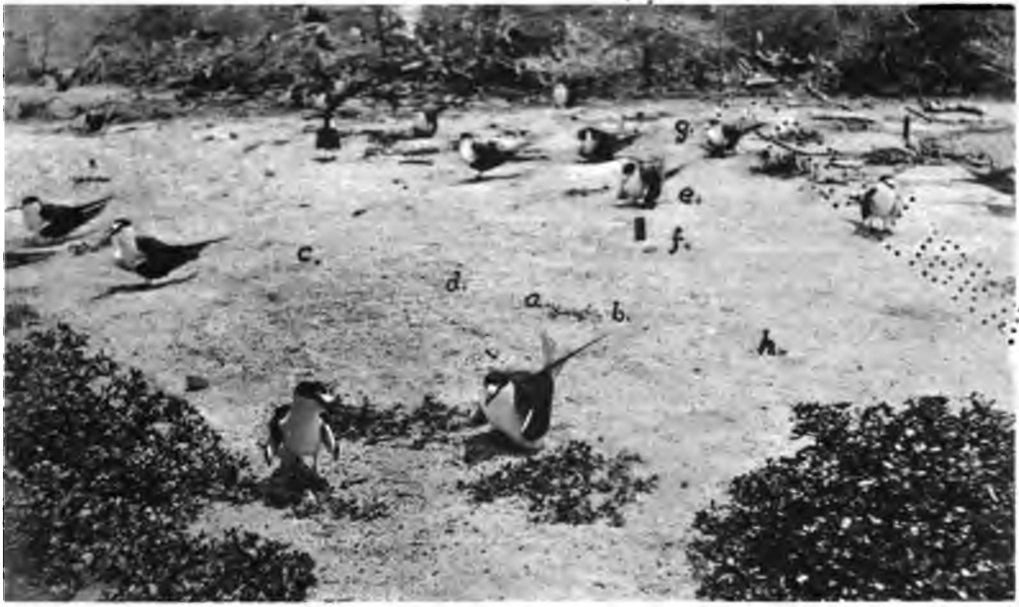

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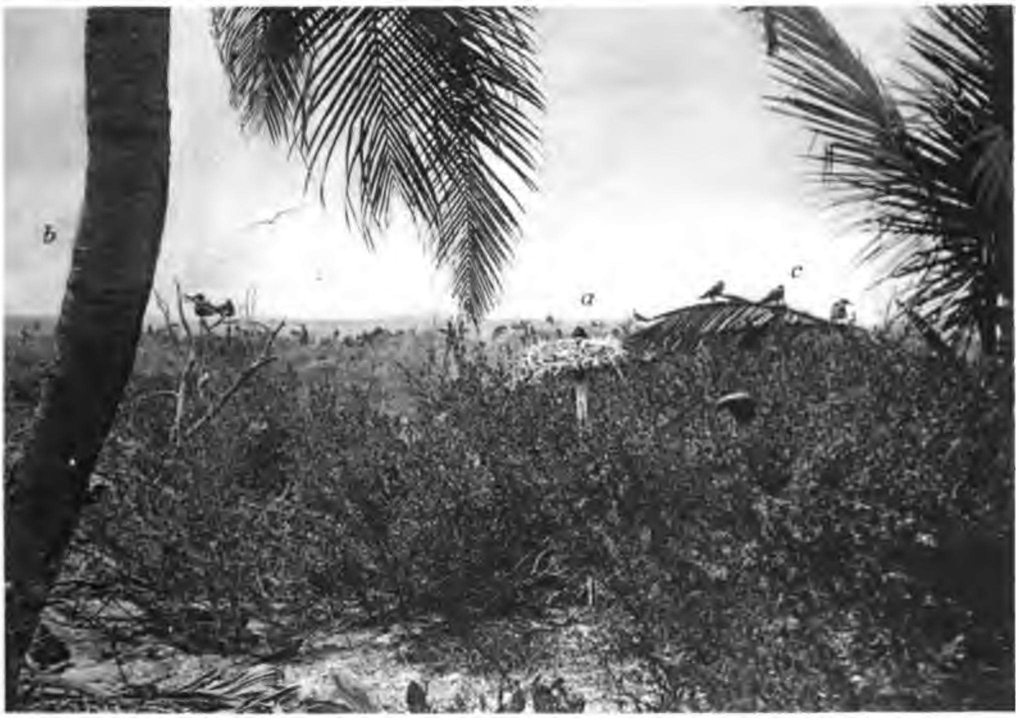

NESTING LOCALITIES OF NODDIES AND SOOTIES.

Fig. 1. Typical nesting area of the sooty.

Fig. 2. The environment of the noddy nest described in experiment 10.

of a stake, *a*, 3 feet farther from the perch, *c*, than its original position. At this time only one bird was present at the nest. It was frightened away and did not reappear for some minutes after the change was effected. It was first identified again as it hovered over the old nest site. Thence it flew to the perch, *c*, then back to the first position of the nest. This was repeated several times.

Without paying the least attention to the nest at *a*, the bird next flew to the large palm, *b*, circled close around its stem, and darted back to the perch. Without alighting here it turned and dropped quickly to the bushes where the nest had been. This was repeated many times until it seemed quite certain that the sight of the large palm furnished the clue to the position of the perch and that the change in direction of flight from the perch to the nest was effected largely in terms of kinæsthesia.

Three points were brought out by these observations. First, the existence of a well-localized perch corresponding to the alighting place of the sooty; second, the use of other very conspicuous objects (in this case, the large palm) as points from which orientation is gained; third, the importance of kinæsthetic-motor habits even in determining the direction of flight. The perch seemed to be recognized partly by its appearance and partly by its relation to the neighboring palm tree.

EXPERIMENT 11.

The nest of a noddy, upon a low clump of bushes, 30 feet from any other noddy nest, was torn from its position and placed 2 feet away at the same level upon the same group of bushes. The nesting bird returned, circled about the nest, and alighted upon it immediately. She covered the egg at once, but seemed a little uneasy. As the nest was not very secure in its new position, its unsteadiness may account for the bird's restlessness.

The nest was next fastened on top of a stake 3 feet above its original position. The bird came back from the westward toward the old position of the nest, caught sight of the new arrangement, and swerved out of her straight course. She circled the nest three or four times, always keeping below the new level at the same height at which she usually flew above the bushes. She then flew out to sea, turned, and came back to the shore. The roof of a small porch on one of the old buildings offered a convenient perch about 20 feet east of her nest and she flew up to this. The most interesting part of her whole reaction occurred here. Instead of alighting on the roof, she hovered beside one corner of it for a moment, then turned and darted unhestitatingly to the old nest site, 3 feet below the nest. She repeated this time and time again, flying to the corner of the porch roof, back a foot above the edge of the bushes past the nest, up into the air, and back to the porch roof. She showed no disposition to alight upon the nest after 15 minutes.

The nest was next lowered to a foot above its original level and 2 feet to the northward of its first position, just at the edge of the clump of bushes. The bird now began to hover above it, but still flew repeatedly to the porch roof and back to the original position of her nest. In 15 minutes she gained courage to alight upon the nest and cover the egg. Half an hour later she was driven off. She returned at once, following the edge of the bushes, and alighting upon the nest.

The nest was next moved 6 feet farther north. The bird returned along the edge of the bushes, hovered for a moment at the old nest site, then flew up and alighted upon the porch roof. From here she flew directly upon the nest, 5 minutes later she returned to the old nest site, from there flew out to sea, then back to the porch roof and to the nest.

On the following day the nest was moved 6 feet farther north. In the meantime the mate of the sitter had returned and both birds had become accustomed to the new position. When it was moved this time, instead of flying out to sea they both hovered about, striking at me, and they alighted upon the nest while I was still adjusting it. I moved it about for short distances in several directions, changed its level several times, and always the birds took it immediately. The visual stimulus of the nest seemed to have become the principal factor in orientation. To test this the stake supporting the nest was replaced by a tripod, the nest itself was covered by a black cloth, and the egg placed on top of this. (Such changes had been found to have no effect when made with nests otherwise undisturbed.) The sitter, the same one upon which former experiments were made, came back past the old nest site directly towards the nest, swerved when 3 feet from it, and returned to the old nest site. This was repeated four times. She then alighted upon the nest, but flew away immediately. Her mate came up and both circled around the nest for some time, but did not alight. The cloth was removed and the first bird covered the nest within five seconds.

The nest was then moved 30 feet to the southward of its original position. The bird came back to the northern site, circled around for a moment, then alighted at the original position of the nest. She looked about, caught sight of the nest in its new position, flew directly to it, and covered the egg. A few minutes later she became dissatisfied and began to fly about, circling from the porch roof to the old nest site, to the nest, and back to the porch roof. She did not settle down before dark. On the following day both birds were observed at the nest, adding sticks to it and apparently quite satisfied. The next day both were gone and were not seen again.

These observations, like the preceding, lay emphasis upon the perch as a conspicuous visual stimulus from which the birds gain accurate orientation to the nest. When this method of reaching the nest failed, the birds came to depend upon the visual stimulus of the nest and were confused by the changes in the appearance of the nest.

The method by which the noddies recognize their nests is very similar to that of the sooties, the only difference being the manner of approaching the nest—in the one case by flying, in the other by walking. The perch has for the noddies much the same relation to the nest as the alighting place has for the sooties. Recognition of the noddy perch seems to be partly in visual terms, partly in the relation of the perch to other very conspicuous visual objects, such as the palm in experiment 10.

Destruction of both the alighting place and nest gave no very definite results. In one instance the birds flew back and forth along the edge of a row of bushes in which the nest and perch had been located, and made swift flights out around a number of tall stakes which had been planted to mark other nests. In almost every instance the destruction of the perch and removal of the nest brought out some antecedent factor in orientation, such as the stakes mentioned above, but these factors were so widely distributed and varied as to be practically beyond experimental control.

ORIENTATION IN APPROACHING THE ISLAND.

In the two experiments recorded it seems clear that the birds gained their first orientation from the visual stimulus afforded by the palm trees and buildings, and from a large number of observations I feel certain that all the birds, on approaching the island, determine their direction with respect to the more prominent visual features of buildings, trees, and bushes. The paths followed by the birds coming in from sea seem to give the best evidence of this.

Figure 2 shows the more prominent features of the island, the buildings and trees at the western extremity, a wide opening in the bushes above the southern beach, and the denser growth of bushes in the central and northern parts of the island. The prevailing winds during the nesting season were from the northeast. When the birds are frightened they run from their nests, leap into the air, and fly against the wind until they reach a height of from 10 to 25 feet, then turn quickly and fly with the wind until well away from the island. If not badly frightened, they turn when 20 to 200 yards in the lee of the island and fly back rapidly against the wind to the region of the nest. Birds in open areas may be kept in sight constantly during the flight and time and time again are seen to follow the same path from and to the nest. The great majority of birds in such short flights return by rather definite pathways indicated by the dotted lines in figure 2. As will be seen from the distribution of the nests, these lines lead directly to the chief nesting areas, and the preponderance of birds following them may be due simply to this fact. In each case, however, the path is near a conspicuous landmark (the buildings and opening in the bushes), and the birds frequently change their direction of flight after passing these, as is indicated by line *d*, figure 2, which is the route followed by one bird in a number of trips to the nest. It seems almost certain that these prominent visual objects are the directing factors in the orientation of the birds when approaching the island.

SUMMARY OF WORK ON NEST RECOGNITION.

The general method by which the birds reach their nests may be summarized as follows: Coming in from the sea, they direct their flight by the more conspicuous features of the island, the buildings, prominent bushes, etc. From these the direction is taken along the shore-line, or the edge of the cleared nesting area to the alighting place, which also offers prominent visual stimuli. From this the path to the nest is followed, either by a series of visual-motor habits built up around other nests, débris, etc., or by a series of kinæsthetic-motor habits irrespective of external stimuli. Study of orientation at night is practically impossible, both because of the difficulty of identifying the birds and, chiefly, because of their increased timidity. During the breeding season, however, the nights are never so dark as to render the chief landmarks invisible at close range and, with direction gained from these, the birds' kinæsthetic-motor habits are adequate for further orientation.

The study of orientation in the nest locality has given no positive evidence upon the method of orientation at greater distances from the nest, but it does furnish two negative points of some importance. First, in the nest locality the birds are dependent upon visual and kinæsthetic habits for orientation and show no evidence whatever of the possession of any special sense of locality, such as a magnetic sense, functional within short flights. Second, kinæsthetic-motor habits are formed with no such rapidity as to suggest that the birds can retrace a path by memory of its successive directions and distances when these have been experienced only once. As in all animals, vision tends to be replaced by kinæsthesia as habits become fixed, but the process is relatively slow and plays no great part in orientation.

RECOGNITION OF THE YOUNG.

Closely related to the problem of orientation and recognition of the nest in the terns is that of the recognition of the young, and in this respect the two species show much greater differences than in nest recognition. The noddies do not distinguish their own young from other young noddies and I have been unable to discover any difference in their active behavior toward either strange noddy or sooty young.

Experiment 12.

I placed a sooty chick, 24 hours old, in the nest of a noddy, taking out the noddy egg which was just hatching. The noddy came back to the nest and covered the young sooty immediately. I watched the nest at frequent intervals throughout the day. The noddy brooded the young sooty constantly, but was not seen to feed it. On the second and third days the noddies continued on the nest, but were not seen to feed the sooty, which on the third day was considerably smaller than other chicks of the same age. On the fourth day, when the noddies were driven from the nest, the chick was found dead, apparently from starvation. Another sooty chick, 4 days old, was placed in the nest. The noddies continued to brood it for 3 days. On the fourth day the chick was dead and the noddies had abandoned the nest.

The noddies accept sooty chicks in exchange for their own young of any age, as was determined by a number of such substitutions. In no case, however, was a noddy seen to feed a young sooty. Apparently the peculiar behavior of the young noddy is required to call out from the adult the instinctive act of regurgitation and feeding.

Experiment 13.

Two 2-day old noddy chicks were placed in a nest which already contained a 3-day chick. One of the younger chicks was white, the other black. The older chick was black. The adult noddy returned and covered the three chicks immediately. The nest was observed regularly for 15 days, when the work was interrupted by heavy storms. The three young chicks were fed by the single pair of adults and throve as well as chicks which were alone in the other nests. On the eleventh day one of the chicks disappeared. The others were still in the nest when observations were interrupted.

During the first days after the hatching of the egg the noddies do not distinguish their own young from those of other birds and react to them only because of their presence in the nest. On the fourteenth day, or earlier, the young noddies leave the nest and lie hidden in the bushes during the day. In the evening they are fed, returning to the nest to meet their parents. Watson states that at this time the noddies distinguish their own young. I have no clear evidence upon this subject, but it seems probable that, as in the case of the sooties, the recognition is rather due to a dovetailing of the habits of parents and young than to a visual or auditory recognition.

Unlike the noddies, the sooties give prompt reaction both to the appearance of the chicks and to the number of chicks in the nest. They will not usually accept young noddies under any circumstances. In one instance a sooty which had been given a noddy egg hatched it and brooded the chick for a few hours in the morning, but in the evening both adult and chick were gone. Usually where a young noddy is placed in a sooty nest the old bird throws it out and drives it far away into the bushes. The reaction is to the visual stimulus,* and is purely instinctive, as is shown by such results as the following:

Experiment 14.

(*a*) I interchanged a sooty egg, just ready to hatch, and a 24-hour chick. The parent of the egg accepted the chick immediately. The other hesitated in covering the egg, looked about, walked to and fro for several minutes, and finally settled down upon the nest.

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*Figures of young noddies and sooties are given by Watson, *opus cit.*

(*b*) I replaced a pipped sooty egg with a young noddy. The sooties attacked the young noddy and drove it from the nest. A third sooty from another nest came and helped in the attack and I was forced to interfere to save the chick's life.

Such reactions are by no means invariable. A sooty will sometimes refuse to accept a sooty chick in exchange for its egg or again will fail for some minutes to notice the presence of a young noddy in its nest; but in general the different appearance of the chicks of the two species calls out different instinctive behavior in the adult sooties.

The greatest variation in the behavior of the adult sooties occurs in their reaction to strange chicks of their own species. Ordinarily they do not distinguish between their own young and other sooty chicks of about the same age during the first few days after hatching.

EXPERIMENT 15.

I replaced a 3-day chick in a nest with another of the same age. The parent returned to the ground near the nest, rushed forward, and threw out the nearest chick (her own), drove him into the bushes, then walked back and covered the other. I placed the abandoned chick in a nest with another of about the same age. One of the parents of this chick returned and accepted both young. Three days later both chicks were still in the nest.

Chicks from 1 to 4 days of age may almost always be interchanged without inducing any marked change in the behavior of their parents. Many such exchanges were made and almost without exception the changelings were adopted without hesitation. Until the age of 4 days the sooty chicks are not recognized individually by their parents. At about that age a change takes place in the behavior of the young sooty. Before this time it feigns death when attacked by adult birds or when removed from the nest to strange surroundings. On the fourth or fifth day it becomes much more active, attempts to crawl out of the nest and hide in the bushes at the experimenter's approach, and attempts to run away when attacked in the open by older sooties. After the age of 10 days it spends most of the daylight hours lying hidden among the weeds and bushes near the nest and comes out only in the evening to receive food from the parents. With its increasing activity it seems to form a set of habits with respect to its nest very similar to those of the adult birds. In its own nest it lies quiet when attacked by strange adults, which happens frequently, for the sooty rarely misses an opportunity to take a sly dig at her neighbor's chick; but outside its own nest the chick, after the fourth day, scrambles away actively when attacked. This seems to furnish the first criterion by which the adults recognize their own young.

EXPERIMENT 16.

(*a*) I interchanged a 1-day and a 6-day chick. The parents at both nests were much disturbed, refused to cover their nests, and poked the young ones with their beaks. The younger chick lay still in the nest and after a short time seemed to have been adopted. The older chick started to run away and was immediately attacked savagely and driven away among the bushes.

(*b*) I exchanged a 3-day and a 5-day chick. The younger bird was accepted immediately by the parents of the other. They did not seem to note the change. When the adults returned to the other nest the 5-day chick ran away. They attacked it at once and drove it away to a distance of 4 feet, where it received so much abuse that it gave up and refused to run further, feigning death. I returned it to the nest. The adults examined it and pushed it away roughly. This time it lay quite motionless, however, and the older birds, after driving away a trespasser, adopted it.

The tendency of these chicks to run away from the strange nests no doubt determined the parents' final action toward them. In the first experiment recorded here, the difference in the appearance of the chicks, differing in age by 5 days, was sufficient to cause some disturbance in the behavior of the parents, but was not great enough alone to cause the rejection of the chick.

On the seventh or eighth day after the eggs hatch, the birds begin to distinguish their own chicks from younger or older ones by their appearance alone.

EXPERIMENT 17.

(*a*) A 2-day chick was placed in a nest instead of the 7-day one which belonged there. The adults pulled it out of the nest and forced it to crawl away. It was immediately adopted by a bird whose nest had been robbed of a young chick upon the previous day.

(*b*) A 1-day chick was placed in a nest instead of an 8-day chick. The parent of the 8-day chick returned and refused to cover the nest for 10 minutes. She continually pecked at the chick, although not savagely. When she showed a tendency to leave the nest, I replaced the young bird with one 3 days old. The parent returned, pecked the chick, and when it started to run away, attacked it furiously. Her own chick was replaced and accepted at once. After a time I substituted a 10-day chick for this one. It was attacked and driven away at once.

The parent sooty here seemed to distinguish its own young, 8 days old, from 1-, 3-, and 10-day chicks which were substituted for it. But the recognition at this time is by no means certain, as is shown in the following observations:

EXPERIMENT 18.

A 6-day old chick and a young egg were interchanged. The parent of the egg drove the chick away immediately. The nest from which the chick was taken was under a clump of bushes. The owner of the nest examined the egg, came out from under the bushes, went back and covered the egg, then came out again. She began to show an interest in the cries of her chick, which was being abused by the egg parent about 3 feet away. She went over and defended the chick, and finally covered it, about 4 feet from her own nest.

I next substituted a 5-day sooty for the egg and replaced the 6-day chick in the egg nest. Its parent returned and found the egg parent attacking it. She rushed to its defense and covered it near the egg nest. Soon she caught sight of the young bird in her own nest. She went over to it and, after looking at it carefully, drove it out of the nest. I replaced it. She returned and accepted it.

Her own chick was put back in the egg nest. She returned, defended it and covered it, about 2 feet from her nest, paying no attention to the strange chick in her own nest. The chicks were then interchanged, the 5-day one being placed in the egg nest and the 6-day one in its own nest under the bushes. The old bird returned and defended the 5-day chick stoutly against the attacks of the egg parent. She followed it for several feet as it ran away and finally covered it. Her own chick caught sight of her and began to squall. She was very much disturbed, got up and started toward it, turned back, and after much hesitation finally went to her own chick in answer to its vigorous cries. As the 5-day chick was always silent this may have furnished the basis for discrimination.

I placed a chick a very little larger than the 5-day chick in the nest under the bushes and the 5-day chick in the egg nest again. The parent started to defend her own chick in a half-hearted manner, caught sight of the chick in her nest, went to it and covered it. A moment later she drove it out of the nest and stood for 5 minutes in the empty nest. I put both chicks in her nest. She pecked the larger, but as it did not run away she covered both.

Half an hour later both chicks were still in the nest. I placed the strange one in the egg nest, where it was promptly attacked. Its foster-mother paid no attention to it, but went to her own chick and nest. I interchanged the chicks. She rushed to defend her chick, covered it, and paid no further attention to her own nest.

The reactions of this adult bird are rather conflicting and hard to interpret, as is true, indeed, of much of the behavior of the birds in tests upon recognition of the young. Seemingly, there is here the beginning of recognition of the chick, based in part upon its appearance, in part upon its "feel" in the nest, its cries, and its reactions to the parent. None of these alone seems sufficient to form the basis of an absolutely positive recognition, and it is probable that the conflicting behavior of the bird is due to the imperfect integration of some such groups of impulses as the following:

(1) Positive reaction to the appearance of the nest and its contents, and to the nest locality.

(2) Disturbance of this caused by the changed appearance of the young and leading to greater sensitivity to other stimuli.

(3) Postive reaction to feel of chick in the nest; this likewise disturbed by the substitution of the larger chick.

(4) Positive reactions to the cries of the chick.

(5) Defending reaction to the situation, *chick attacked by adult.* (For more detailed examples of this see p. 83).

(6) This defending reaction is established as a habit which temporarily exceeds even (1) in force.

All these factors are apparent in the activities of this bird and stand out more or less clearly in the reactions of most of the sooties to their own and to other young. Recognition of the young at this stage thus appears to be the result, in part, of the pattern of visual and tactual stimuli offered by the chick; in part, of the behavior of the chick in the nest region (experiment 16). Complete recognition is the result of a complex of many sensory-motor reactions, not merely of a single type of stimulus.

With older chicks, after the tenth day, it is almost impossible to carry out observations unless full time may be devoted to them. They lie hidden among the bushes during the greater part of the day and come out to their nests only at the return of their parents. They are extremely wild and run to cover whenever the colony is disturbed. They show a familiarity with the nest region almost equal to that of the adult birds, returning readily to the nest alone, threading their way among other nests and avoiding the attacks of strong adults. From such observations as I have been able to make I believe that the chicks usually take the same cover and that both chick and parent become perfectly familiar with the details of the most direct path from this to the nest, meeting one another at various points along the path and reacting to one another, at least in part, by virtue of their presence in this familiar neighborhood.

Watson has shown that when the appearance of adult birds is completely altered, as by painting their breasts and head with brilliant colors, they are at first rejected by their mates, but this rejection is not permanent and the disfigured birds are finally accepted by their mates by reason of their persistence in their normal activities in the region of their nests. The "recognition" through the interrelation of habits overcomes the disturbance produced by the changed visual situation. For the recognition of the young, the same complex of reactions must be established. The visual stimulus provided by the young at the nest calls out the normal brooding activities. A slight change in the appearance of the young interrupts the normal series of activities and leads to trial movements. If the situation remains otherwise unchanged—if the behavior of the young gives the customary series of stimuli—the changed appearance comes to be disregarded.

INSTINCT AND HABIT IN THE NESTING ACTIVITIES.

MODIFIABILITY OF INSTINCTIVE ACTIVITIES.

The activities of the birds centering around the nest during the breeding season may be roughly divided into mating, selection of the nest site, construction of the nest, laying, incubation, and the rearing of the young. During each of these periods a special group of instinctive acts is called into play and the behavior of the birds is modified quite suddenly at the transition from one period to the next, as in the sudden appearance of the constant brooding activities after the egg is laid. Watson found that birds which are quite timid become aggressive as soon as the egg is laid and either refuse to be driven from the nest or attack intruders actively. He was able to induce an early appearance of this change in behavior by placing an egg in a newly completed nest, and thus raised the question of the relation of these changes in instinctive behavior to external stimuli and to internal processes.

I have obtained a small amount of evidence bearing upon this question, but the data are fragmentary and a great deal more time may be spent profitably upon this particular aspect of behavior. Owing to the lateness of the season when the work was begun no observations were obtained upon mating or the construction of the nest.

Experiment 19.

After some difficulty a newly completed noddy nest was found. The building activities of the owners had almost ceased, but no egg had been laid and the birds were not occupying the nest regularly. At the first observation, one of the birds was perched on a dead limb near the nest and the other was not in the neighborhood. A noddy egg was placed in the nest. This was early in the morning. No change in the activity of the bird at the nest was observed during the day. It disappeared occasionally, but did not show any reaction to the egg. The mate was not seen.

On the following morning a bird was found brooding the egg. Its mate was on the dead limb near by. When I approached both birds defended the nest, the one on the perch flying into the air and striking at me, the sitter refusing to leave the nest. I caught the latter and marked it with a spot of paint. The marked bird was occupying the nest when it was observed later in the day.

On the third day only the unmarked bird was seen at the nest. It spent the day sitting on the perch or on the edge of the nest, paying no attention to the egg.

On the fourth day the marked bird was again observed at the nest. Both birds were upon the nest, the marked one brooding the egg, the other standing on the edge of the nest. Both flew up at my approach. The marked bird returned immediately and covered the egg. The unmarked one returned, hovered about for a short time without alighting, and then flew out to sea.

On the following day the marked bird was observed on the perch. At this time the unmarked bird was on the nest over the egg. For as long as I watched, this bird did not assume the brooding position, but stood upright and turned about, moved to the edge of the nest, and flew away rapidly when disturbed, thus showing the behavior of the layer rather than of the sitter.

The marked bird was on the nest for the greater part of the sixth day. The unmarked bird was seen on the edge of the nest, but did not cover the egg.

On the seventh day a second egg had been deposited and the unmarked bird spent the day in brooding the eggs. After this time the birds seemed to take turns regularly in brooding the eggs.

In this case it seems clear that only one of the birds was stimulated to the brooding phase of activity by the sight of the egg. The other retained almost wholly the behavior of the layer up to the time when the second egg was deposited. There can be little doubt that this second bird was the female, that the stimulus in the case of the male was purely visual and tactual, while in the case of the female the act of laying was necessary before the brooding phase could appear.

It is generally stated by the natives of the region that the sooty will lay a second egg if the first is taken from the nest. I was unable to verify this. The eggs were taken from 10 nests and in no case was a second egg deposited; the nests were all abandoned after a few days. However, none of these nests was less than a week old, and it is possible that the loss of the egg at an early period may serve as a stimulus to further oviposition.

An attempt was made to find out how long incubation might be interrupted by removal of the egg without leading to the abandonment of the nest. Eggs were taken from a number of nests and returned at regular intervals, from 6 hours to 4 days. Brooding activities were resumed by the birds after 4 days. The experiment had to be interrupted here because of stormy weather.* From rough observations, however, I believe that after a week's interruption the birds will not resume incubation. The time is certainly less than the time required for the loss of the brooding instinct of birds in captivity,† as might be expected from the greater opportunity which free birds have to form new habits toward the colony.

After the hatching of the egg the parental instinct seems to be even more dependent upon the stimulus of the chick in the nest. In some cases nests from which the chicks were removed seemed to be wholly abandoned after 48 hours.

The second marked change in the behavior of the nesting birds occurs at the hatching of the eggs. The incubation period of the noddies is given by Watson as 32 to 35 days, that of the sooties as 26 days. I made attempts to shorten and to lengthen the time required for incubation in order to test the extent to which intra-organic factors are concerned in the changes from incubation to brooding activities. The experiments are very unsatisfactory, chiefly because the age of very few nests was known.

Substitution of young chicks for noddy eggs of any age was not followed by any marked change in the behavior of the adult birds. They were never seen to attack the chicks, but I could not determine how soon such chicks are fed. It seems certain, however, that the incubation period of the noddy may be shortened by at least one-fourth without serious interference from an intra-organic rhythm.

Attempts to shorten the incubation time of the sooties have not been carried out fully, but there is more evidence that the length of the incubation period is determined, to some extent, by internal factors. Parents whose eggs are less than two weeks old will not adopt young chicks. The data at hand are not conclusive beyond this point. Adults whose eggs are pipped will sometimes refuse to accept young birds in exchange for them, but usually during the last week of incubation such changes may be made without difficulty.

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*Experimental work with the colony was made almost impossible during the last 10 days of June, at a time when the young birds were in the most interesting stage of development. High winds and heavy rains, with a considerable lowering of the temperature, made it advisable to disturb the colony as little as possible, as the birds frightened up from the ground were instantly blown far out to sea and at times could not regain the island for hours.

†See page 43 of this volume.

The period of incubation may be lengthened also to some extent, but this differs in different birds and its limit was not determined.

In 10 nests younger eggs were substituted for pipped ones. After 2 days one of the nests was abandoned. During the following 5 days 6 of the eggs hatched. The remaining birds were still sitting at the end of 7 days, when observations had to be discontinued.

A dead egg was substituted for a pipped one, somewhat earlier in the season. Upon the following day it was found that the parents had adopted a 3-day old chick and were brooding both it and the egg.

This observation and the abandonment of the single nest in the other experiment suggest that the length of the incubation period is conditioned by an internal rhythm, which does not determine, however, an exact period of 26 days, but permits a range of variation of 2 weeks or more around this period.

INTEGRATION OF COMPLEX HABITS.

Two of the most striking features in the colonial life and behavior of the terns are the enormous number of habits which they exhibit and the disconnected, impulsive character of their activities. The number of habits involved in the process of orientation has been illustrated in the earlier experiments. By the time that the experimental work had been carried far enough to give an insight into the mechanism of orientation the eggs were all laid and the birds had been reacting to the situation at the nest for some weeks. Hence there was little opportunity for study of the formation of the habit complexes. In general, as might be expected in a colonial bird, the most definite and firmly established reactions are associated with other birds or their nests. The chief landmarks used by many sooties for the final location of their nests are the nests of their neighbors, and it is apparent that the presence of these neighbors, defending their nest areas, tends to give a greater stimulating value to the nests. The birds whose nests were in very crowded areas showed a much lower plasticity in adapting to changed conditions than those whose nests were somewhat isolated, hesitating to occupy nests only a few inches from their own nest sites and offering little defense of such nests against trespassers. The behavior of the birds suggests that in the early part of the nesting season exchanges of nests must be of relatively frequent occurrence. An interesting example of the diffidence of the birds in appropriating new nests is given in the following:

Two sooty nests, 18 inches apart, were obliterated and both eggs were placed in a new nest half way between them. The parents of both eggs returned to their nest sites, missed the eggs, and began to look about for them. One caught sight of the eggs in the new nest and covered them. The other at once drove her off and took the nest. The first, after standing for a few moments at her nest, returned to the new nest and drove off the second. This was repeated several times, the bird occupying the nest offering little resistance to the attacks of the other but returning fiercely to the attack after a visit to her own empty nest. Finally one bird rolled an egg back to its nest and both settled down contentedly.

In small matters, such as changes of a few inches in the position of the nest, changes in the appearance of the egg, young, or nest, the habits of the birds may be quite readily modified, but this seems to hold true only within certain limits. Many attempts were made to shift nests to the edge of the beach with the purpose of transferring them to rafts in the hope of ultimately transplanting a part of the colony to other keys, but however slowly such shifts were made (6 inches or so per day) the nests were either abandoned when moved 4 feet or less from their original position, or the eggs were rolled back as fast as they could be moved forward.

NOTE.—This moving of the egg back to the original position of the nest has been mentioned before in connection with other experiments. It might seem to involve very complex processes, memory of the relative position of the egg and nest and an attempt to restore their relation. I watched the entire procedure in a dozen or more instances and believe that there is little implicit behavior involved in it. The bird, returning to the empty nest, misses the egg, looks about, and catches sight of it a few inches away. She starts towards it rapidly, but goes more and more slowly as she approaches, sometimes turning back before reaching it. Perhaps after several such hesitating starts she gets close to the egg, stops as soon as she can reach it with her beak, and rolls it back under her body. In this way the egg is moved for 2 or 3 inches at each trip from the old nest site to the egg. That it is moved in the direction of the old nest site seems to be the result of the fact that the bird always faces away from the latter as she approaches the egg. There is no real evidence of implicit behavior in this case, even of a delayed reaction in which orientation is held as the egg is moved.

In all its activities, where reaction to a new situation is involved, the behavior of the birds has a peculiarly impulsive character. One group of stimuli seems to gain momentary control and determine the bird's reaction in spite of contradictory elements in the situation as a whole. If a chick is taken from its nest and put down among strange adults they are at once attracted by its cries and crowd around it. Several of them attack it and immediately others rush forward to defend it. The fight becomes general and may give the chick a chance to escape. After a time some of the adults are driven away and leave the victors to strut about. If one of these catches sight of the chick, he attacks it and the fight is soon renewed. I have seen the same bird alternately attack and defend a chick through a number of fights; the sight of the strange chick calls out movements of attack; the sight of an adult attacking a chick calls for defense of the chick. Young chicks, when attacked by adults, either feign death or sprawl about helplessly, without being able to escape. In the latter case they sometimes force their way under the body of the adult. When this happens it practically always produces a marked change in the behavior of the adult bird. His aggressive attitude drops away suddenly, he shuffles about for an instant, looks down at the chick, tucks it under him with his beak, and assumes the brooding position. If he is at some distance from his nest this brooding reaction is of short duration; he soon grows restless, gets up and turns around several times, and finally returns and attacks the chick with renewed savagery.

The same lack of coördination in reactions to complex situations is seen in the choice between two nests, in the re-orientation in the path to the nest, and in the reaction to changes in the appearance of the path. The reactions are to separate groups of stimuli and there is clearly no analysis of the situation as a whole. The birds do what a man would only consider doing under like circumstances; that is, they carry out in overt activity many of the same processes which in man are restricted to the language mechanism. In subjective terms, they show little or no evidence of "ideational processes" in their activities.

STUDIES ON THE SPECTRAL SENSITIVITY OF BIRDS.

BY J. B. WATSON.

STUDIES ON THE SPECTRAL SENSITIVITY OF BIRDS.

METHODS OF STUDYING SPECTRAL SENSITIVITY.

In the literature bearing upon the homing sense (distant orientation) one meets with the theory[*] that possibly those animals in which such a function resides possess retinas sensitive to extremely long wave-lengths. It is further supposed by the adherents of such a view that these long waves follow the surface of the earth.[†] As a consequence, any animal with very keen vision, having a retina sensitive to them, could directly respond to the visual stimulus of a distant goal (côte, nest, etc.), the curvature of the earth by hypothesis not interfering with the continuity of vision. Such a theory, while speculative in the extreme and without good physical support, can not be dismissed without some experimental tests, especially in view of the fact that no hypothesis of return (logically) simpler than this has yet been advanced.

During the spring of 1912 we decided to make a careful test of the limits of spectral sensitivity in the noddy tern and in the sooty tern. It is clear that the above theory has no standing if it can be shown that the animal under consideration has a spectrum coextensive at the red end with that of man ($\lambda = 7600$). In order to make the work more complete we purchased some chicks (of mixed breed) for testing in the same apparatus. We set up the apparatus, consisting of a large spectrometer with suitable compartments for controlling the responses of the birds, in the Marine Biological Laboratory of the Carnegie Institution of Washington, Tortugas, Florida. After capturing and rearing 12 young noddies and 12 young sooties and constructing a rather elaborate dark room, we found that the small electric-light plant which we had installed could not be run with sufficient steadiness for use with the Nernst lamp. We finally decided to abandon the experiment at Tortugas and to remove the apparatus and the birds to the Psychological Laboratory of The Johns Hopkins University.

The birds arrived safely, standing the long journey by rail very well. They were placed in a large yard and fed twice daily with chopped fish. For some reason they did not thrive, and died one by one. By the time the apparatus could again be made ready all the terns had died. There remained only the three chicks brought from Tortugas. We thought it distinctly worth while to test them, since they are day birds and especially sensitive to red rays, as has been shown by Hess.[‡]

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[*] Faculté de direction du pigeon voyageur. Ann. de Psych. Zool., I, 1901, p. 22; II, 1902, p. 48. The above article was written by Hachet-Souplet. Duchátel's view appears in the article in a series of letters.

[†] Duchâtel and Hachet-Souplet, as has been pointed out by E. Branley, in the article referred to above (II, p. 57), are apparently not familiar with the properties of light. Duchâtel at least draws an analogy between the Hertzian waves and the infra-red rays. Now the Hertzian waves do apparently follow the surface of the earth (over water at any rate; as to their course over a mountainous region there seems to be some question). But the Hertzian waves have a length varying from a few centimeters to many meters, and are not to be compared with the relatively extremely short infra-red rays which may be obtained from prismatic spectra. Contrary to Duchâtel, the violet rays would come nearer fitting his theory, since they suffer greater refraction by the different layers of the earth's atmosphere. Had his theory been based upon ultra-violet rays rather than the infra-red, it would have had slightly better physical support.

[‡] Hess, C., Ueber Dunkeladaptation bei Hühnern und Tauben. Archiv f. Augenheilkunde, 57, 298; also 57. 317.

The experiment naturally falls into two parts: first, accurate determination of the limits of the spectrum at the violet and red ends; second, plotting of the sensitivity curve for monochromatic light. At the end the attempt is made to compare these findings with those obtained from similar tests upon man.

A very large spectrometer was used, the ground plan of which is shown in figure 8. It consists of the source L, a Nernst automatic lamp burnt at 110 volts, D. C. The lamp was controlled by regulating the amperage (the ammeter reading to $\frac{1}{10}$ of an ampere); a single achromat condenser gave an image of the source upon the slit S (this slit is accurately controlled by a micrometer screw); the collimator Cm, which is a compound 4-inch portrait lens; the dense flint-glass prism P, with 4-inch face compound portrait lens O, used as the objective, and the slit S_2, which was mounted upon a carriage controlled by a micrometer screw. The slit system was directly calibrated in terms of wave-length, so that any possible region could be immediately admitted to the dark room.

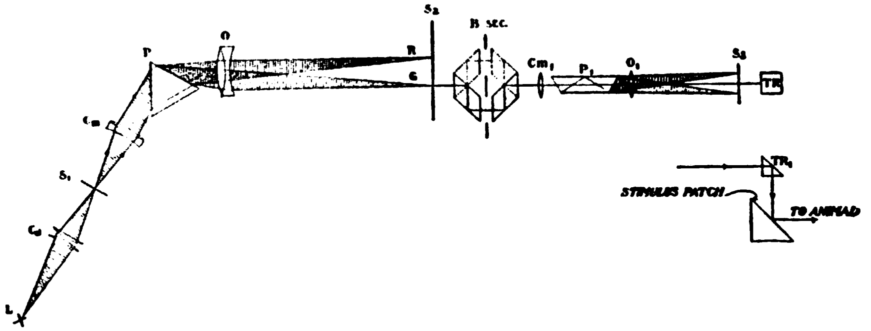

FIG. 8.—Ground Plan of Double Spectrometer. L, source (Nernst); Cd., condenser; S_1, slit; Cm., collimator; P, dense flint glass prism; O, objective; S_2, selecting slit; B. sec., Brodhun rotating sector; $Cm._1$, collimator for auxiliary spectrometer; P_1, direct vision prism; O_1, objective for auxiliary spectrometer; S_3, final selecting slit; TR., total reflection prism throwing light on plaster surface. The small sketch at the right is a vertical section through T. R., showing the way the beam is finally projected upon the plaster surface (stimulus patch).

For the work on limits the Brodhun sector (B. sec.) and the auxiliary spectrometer shown in the diagram were not used. These were employed in the second part of the work—the determination of the relative stimulating effect of the different spectral regions.

The Brodhun sector is too well known to require detailed description. It consists of a series of rotating prisms which revolves the light around a stationary sector. It permits of the immediate control of the intensity of the light without stopping the motor for the needed adjustment. The sector openings are controlled by an arm extending from the housing of the sector. An arbitrary scale in millimeters running from zero, where the sector is fully closed, to 140, where the sector is open at the maximum allowed by its construction, permits one to adjust the intensity of the light with great accuracy.

For reasons which will appear in the text, it was found necessary, in the second part of the work, to secure monochromatic light practically free from admixture with white light. This can not be secured with a simple spectrometer system. Accordingly, after a given band of light had been selected by the slit S_2, it was passed through a second spectrometer, of which Cm_1, in the drawing, is the collimator, P_1 the direct vision prism, O_1 the objective, and S_2 the final slit. The total reflection prism TR throws the beam vertically down on the plaster-paris surface (stimulus patch 3 cm. × 5 cm.), which is placed in the compartment in which the response of the animal is obtained. Issuing from this second spectrometer system is a band of monochromatic light, which, when examined with a pocket spectrometer, shows no further resolution.

In determining the curve of the relative stimulating value of light of different wave-lengths the bands of monochromatic light were equated in energy. Since thresholds were involved, the calibrated selenium cell, by means of which the energy was determined, was put 10 cm. above the stimulus patch and directly in the path of the beam. A. H. Pfund's method of calibrating with this cell will be found in Yerkes and Watson.* Even calibration before diffusion did not give a beam sufficiently low in intensity for direct use in threshold work. It was found necessary to introduce a wedge of smoked glass behind the final selecting slit. In the yellow-green, green, and blue regions a very dark glass was required; in the yellow and orange regions one very much lighter was required. Finally, in the red region no glass at all was required. Since these glasses were inserted after calibration, it was necessary to send them to the Bureau of Standards for calibration as to absolute absorption at the different wave-lengths employed in this work. The curve (fig. 10, p. 98) contains the proper corrections. When the appropriate smoked glass was inserted the threshold for the animal was found to lie well within the range of intensities offered by the Brodhun sector.

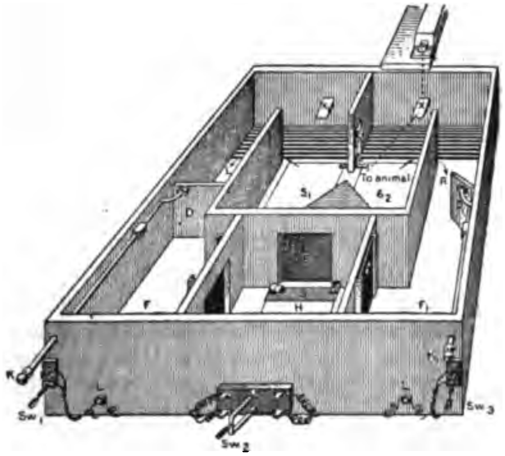

FIG. 9.—Control Box. H, home box; C, response chamber; F, F_1, food compartments; X, X_1, stimulus patches; S_1, S_2, platforms causing lights L, L, to wink; S, platform causing both lights to wink simultaneously; D, D_1, doors leading to food compartments; K, K_1, knobs controlling these doors.

The animal's reactions were taken in the apparatus shown in figure 9, which consists of a large box, 94.5 cm. in length by 74 cm. in width by 25 cm. in depth. It is divided into a home compartment H, 31.5 cm. in length by 25 cm. in width, and a response chamber C, 30.5 cm. in width, which is partially separated into two smaller compartments by a partition. The length of the partition is 25.5 cm. The distance from the door leading into the response chamber to the stimulus patch is 69 cm. The distance between the stimulus patches is 25 cm. The dimensions of the face of the stimulus patch are 3 cm. by 5 cm. The other divisions of the box are not important.

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*Methods of Studying Vision in Animals, Behav. Mono., 2.

It can readily be seen that the box offers two alleys which lead into food compartments, F and F_1. Two doors, D and D_1, permit one to confine the animal in the proper food compartment. By a special mechanism the doors can be closed after the passage of the animal from without the apparatus by pulling knobs K and K_1. Two doors lead from F and F_1 into H. It is thus possible to work with the animal without touching it and without being seen by it.

By means of a special signaling device the movements of the animal can be recorded without the necessity of watching it. Two miniature lamps, blackened except for an opening about 1 mm. in diameter, are electrically connected with the platforms S and S_1 and S_2. When the animal crosses S and goes into the response chamber both lamps are caused to wink (break circuit). If he then crosses the right-hand platform S_2, the right lamp goes out until the reaction is completed and the animal turns into R. If the animal goes across S_1, the left lamp goes out, etc. In the drawing the stimulus light falls upon the right stimulus patch X; consequently food may be obtained by passing around R through the open door D_1. It will be noted that the door D is closed. If the animal makes the wrong choice it must pass S_1, around into alley L; there finding the door closed, it must retrace its steps and pass S_2, into R through D. The apparatus as a whole can be shifted so that the light may be made to fall either upon X or X_1 at will. Although arranged for punishment by electric shock, punishment was not used in the experiments upon the chicks.

THE LIMITS OF THE CHICK'S SPECTRAL SENSITIVITY.

The experiments were carried out upon three chicks. Experimentation began on August 30, 1912. On that date the chicks were exactly 30 days of age. Before actual tests were made the animals were forced to go through the complete reaction they would have to use during regular experimentation; that is, they were at first confined in the home box, then admitted to the reaction chamber, and then forced to go to the right or left food compartments at the will of the experimenter. These preparatory exercises were conducted in a well-lighted room. One of the interesting things appearing in these tests with both chicks and terns was the failure of the birds to learn readily to pass around into the alleys L and R. Some rats which the writer tested in the same way learned to make these turns in a few trials. It took nearly 3 weeks to get the birds to run rapidly from entrance into the stimulus chamber around to the food. When they had learned to make the turns, regular tests were begun. These consisted in responding positively to the compartment illuminated by the monochromatic light (or negatively to the dark compartment).

The chicks were brought into the dark room in a basket and allowed to remain in complete darkness for 10 minutes. Then a 16 c. p. tantalum light placed 1 meter above the center of the home box was turned on and a chick was placed in H. The chicks are designated by D, R, and G. D was always experimented upon first; then in order, R and G. The state of adaptation for the three chicks was thus not quite the same.* As soon as a chick was placed in H the tantalum light was turned out. Five seconds later (by metronome) the door to the reaction chamber was opened. The chick then passed out and reacted either positively or negatively to the light. When the animal had immediately, or after errors, finally correctly responded (*i. e.* positively), as shown by causing the proper light to wink (p. 90), the tantalum light was again turned up. After feeding for 3 seconds the animals were allowed to pass again into H through one of the side doors. The light was again turned out for 5 seconds and the test repeated. At first only 6 to 8 tests were made. The number was then increased to 10 and sometimes in control work to 15 to 20. In the following tests no effort was made to control the energy of the stimulus. The light falling on the plaster surface was very intense—the maximum afforded by the spectrometer at any given wave-length. We planned to test the animals first near the center of the spectrum, $\lambda = 5480$, and then to pass on in the red region until a limit to response was reached; next to retrain on $\lambda = 5480$, and then to pass to the violet region, continually decreasing the wave-length until the limit was reached. Table 23 gives a summary of the tests at $\lambda = 5480$, showing that the retina of the chick is sensitive to $\lambda = 5480$, and furthermore, that the chick is *distinctly positive* to light.

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*And yet no marked differences in sensitivity of a progressive kind were noted. The use of the white light after every response, as above described, probably kept adaptation constant in all. The two chicks not undergoing experiments were kept in the room with the apparatus. The wicker basket in which they were confined admitted light with readiness.

TABLE 23.

No. of trials.	Animal.	Per cent right.	Remarks.
29	D	93	Two errors were made on first day.
29	R	90	Only one error after first day.
29	G	95	

LIMITS AT THE RED END.

In order that no useless work might be done in testing the chicks at intermediate points, I next tested them in a similar way at $\lambda = 6230$; then at $\lambda = 6520$ and $\lambda = 6825$ (table 24).

TABLE 24.

	No. of trials.	Animal.	Per cent correct.	Remarks.
$\lambda = 6230$	12	D	100	
	12	R	100	
	9	G	100	
$\lambda = 6520$	6	D	83	
	6	R	100	
	6	G	100	
$\lambda = 6825$	8	D	87	Animal badly disturbed, very slow, cried a great deal.
	8	R	87	Considerably slowed.
	5	G	100	After fifth refused to work. Turned slit back to $\lambda = 6520$; animal worked well at this point.

As the animals were somewhat disturbed on the final test, due probably to the low stimulating value of the light, I increased the intensity by opening up the slit in the collimator S_1, with the results shown in table 25. The time of the response was also recorded.* The tests shown in table 25 were made on successive days.

Since the animals were holding to such a high percentage of correct choices, I became suspicious as regards the stimulus to which they were responding. I convinced myself speedily that there were no secondary criteria, such as noise, rotating of the box, etc., which could be responsible for their reactions. The animal would not respond in any definite way when the monochromatic light was excluded. It became evident that the illumination on the plaster surface was responsible for their actions. I next turned the slit far out beyond the limits of the human spectrum (λ = 8000) and found that the animals still reacted correctly. Under the conditions of this latter test the plaster surface was invisible to me, but after darkness adaptation it became faintly visible. This was undoubtedly due to the stray white light present in this simple spectrometer. I had not supposed its intensity great enough to create disturbance in animal work of this kind. Such a source of error is not mentioned in the voluminous works on color responses in animals.

This brought me into consultation with my colleague, Professor A. H. Pfund, who assured me that there was always a large amount of such light in both prism and grating spectra, and that there were two methods of eliminating it: one by putting behind the slit in the objective a filter of such a nature that there would be transmitted only the region of the spectrum desired. In this way all diffuse white light could be eliminated. The other method was to use the purified spectrum of Helmholtz, *i. e.*, to take the monochromatic band as it issues from the first spectrometer and to pass it through another spectrometer. All diffuse white light in the beam so chosen is thrown off into a secondary spectrum. Mention (p. 88) has already been made of the set up of this auxiliary spectrometer.

TABLE 25.

	No. of trials.	Animal.	Per cent right.
λ = 6825	6	D	100
	6	R	100*
	6	G	100
λ = 7000	6	D	83
	6	R	100
	6	G	100
λ = 7195	6	D	83
	6	R	100
	6	G	100

*Evidently increased intensity made response easier.

The first method is not satisfactory for use in experiments where it is necessary to pass rapidly from one region of the spectrum to another. The second method is the only thoroughly satisfactory one in such work as the determination of the relative stimulating value of waves of different length.

Since the work on limits required only two filters—one at the red end and one at the violet—it was at the time decided to be more convenient to use them than to wait for the construction of the double spectrometer. By the time the work on limits had been completed the second spectrometer was ready for use. It is certainly advisable, when the apparatus is at hand, to employ the "purified spectrum," even in the work on limits.

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*The time of all responses was taken from this point on throughout the remainder of the experiment. It is without general significance, so is not given. It aided the experimenter materially in keeping adaptation reasonably constant. As a matter of fact, as the limit is approached, the time increases enormously. The chicks attempted to form the habit of waiting in H until adaptation brought the light over the threshold. This could be checked by waiting until the normal time for reaction had passed, then closing the door, turning up the light for 5 seconds, then turning it out and repeating the regular routine of the test. The time of normal reaction varied from about 2 to 14 seconds.

Pfund has found two filters which work well in the determination of limits. The filter for the red end consists of an aqueous solution of cyanin and potassium bichloride placed in a convenient glass cell with plane parallel sides. Such a cell was placed just behind the selecting unit, which was set at $\lambda = 7000$. This filter transmits 80 per cent of the light from $\lambda = 7000$ up to 1μ, but excludes all light below $\lambda = 7000$. When placed behind the slit, the red surface was clearly visible to me after 20 seconds of darkness adaptation.* The slit in the collimater was set at 0.75 mm. and that in the objective at 0.52 mm. The complete records of the chicks are shown in table 26.

On the following day I set the slit at $\lambda = 7150$ with other conditions exactly as before. The light was quite faint to me. After 5 minutes' adaptation to darkness the red surged in quite clearly.

TABLE 26.

$\lambda = 7000$.	No. of trials.	Position of light.	Response.		Remarks.
Chick D	1	Left	Left	62 per cent	I waited before admitting animal until light was visible to me.
	2	Left	Right		
	3	Right	Right		
	4	Right	Right		
	5	Left	Left		
	6	Right	Right		
	7	Left	Right		
	8	Right	Left		
Chick R	1	Right	Right	88 per cent	I waited before admitting animal until light was visible to me.
	2	Right	Right		
	3	Left	Left		
	4	Left	Left		
	5	Right	Right		
	6	Right	Left		
	7	Left	Left		
	8	Right	Right		
Chick G	1	Right	Right	100 per cent	I allowed this animal to make choice 10 seconds after turning out tantalum light, regardless of whether I could see it. It was below my threshold in nearly all cases when he made his choice.
	2	Right	Right		
	3	Left	Left		
	4	Left	Left		
	5	Right	Right		
	6	Right	Right		
	7	Left	Left		
	8	Left	Left		

Chick D chose correctly 3 times, then made 3 consecutive errors, after which he refused to respond even after long adaptation. I then turned the slit back to $\lambda = 5480$ (green of original training series) and gave him 5 trials; all were correct and the average time of reaction was 2 seconds.

Chick R chose twice correctly and then made three consecutive errors. When tested on green of training series, 5 correct choices were made in an average time of 2 seconds.

Chick G would give only 8 responses; during these 8 trials two errors were made. The animal chose with great difficulty. The average time of this chick was 12 seconds. Since it had made but one error during the whole course of the experiment, and that on the third day of its preliminary trials, I think it fair to call this place $\lambda = 7150$, the red limit under the conditions of the present test. The limit of D is evidently $\lambda = 7000$, while that of R is between $\lambda = 7000$ and $\lambda = 7150$. When tested with light-waves of greater length, no response was obtained.

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*When it appeared it came in a burst of red light. There was no photochromatic interval whatever.

LIMITS AT THE VIOLET END.

After a preliminary test upon green $\lambda = 5480$, in which all choices were correct, the chicks were tested with violet $\lambda = 4500$, with the Nernst as a source. The stimulus was plainly visible to me. Six tests were given each animal, as shown in table 27:

TABLE 27.

	No. of trials.	Animal.	Per cent correct.	Remarks.
$\lambda = 4500$	6	D	100	Clearly above my threshold the moment the light was turned out.
	6	R	100	
	6	G	83	
$\lambda = 4200$	8	D	82	Animal seemed to experience great difficulty. Light above my threshold at end of the 5 seconds.
	8	R	100	
	8	G	100	

Again I became suspicous as to the adequate stimulus, especially in view of Hess's work. In order to eliminate all diffuse and scattered white light I put in a filter of $CuSO_4$ to which an excess of ammonia has been added immediately behind the selecting slit. The thickness of the layer was 1 cm. I first tested with a pocket spectrometer, to see that only violet and bluish-violet rays were admitted. It was necessary to open up the slits, S_1 to 0.75 mm. and S_2 to 1 mm., in order to make the light visible to me. The results are given in table 28.

In order to obtain fairly high intensities in the shorter wave-lengths I found it necessary to substitute the automatic Bausch and Lomb arc lamp for the Nernst.* The filter was arranged as before. The results appear in table 29.

TABLE 28.

$\lambda = 4500$.			
No. of trials.	Animal.	Per cent correct.	Remarks.
8	D	88	Clearly over my threshold at end of 2 seconds.
8	R	100	
8	G	100	

TABLE 29.

$\lambda = 4010$.		
No. of trials.	Animal.	Per cent correct.
8	D	100
8	R	100
8	G	100

On the following day the arc was again used, but as an extra precaution against white light I placed a filter of the same constitution as the above (cupra-ammonium) in front of the slit in the collimator S_1. The pocket spectrometer showed that no light was admitted except the violet rays.

The chicks were first tested with $\lambda = 3950$. It was visible to me at the end of a long adaptation time, but not visible under the conditions offered the chicks.

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*Yerkes and Watson, *op. cit.*, p. 89.

Both D and R broke down completely and took up right-hand position habits. I then immediately gave them λ = 4050, with conditions as in previous tests, with the results shown in table 30.

Evidently under conditions such as I have been describing the violet limit lies between λ = 4050 and λ = 3950 for these two animals. The stimulation was in every case over my threshold. Furthermore, the animals were admitted 10 seconds instead of 5 after turning out the light.

Much to my surprise chick G gave different results. He was tested under the same conditions as D and R with λ = 3950. The light to which he responded was never above my threshold. I give his record in full in table 31. In every trial in which 10 seconds were given, the animal responded correctly. It is evident that the threshold is a flexible kind of thing and dependent naturally upon adaptation. The limit for G for long adaptation is certainly lower than λ = 3950, but for 5 seconds' adaptation at the present intensity λ = 3950 is about the limit.

TABLE 30.

λ = 4050.		
No. of trials.	Animal.	Per cent correct.
6	D	100
6	R	100

On the whole, I think it perfectly safe to conclude that chicks do not have a spectrum shortened at the violet end, nor yet do they show any special sensitivity in the violet. The experiments of Hess* and of Katz and Révész† lead them to believe that the chick is practically blind to blue and violet rays.

TABLE 31.

Chick G. λ = 3950.			
No. of trials.	Position of light.	Animal's response.	Remarks.
1	Left	Left	10 seconds after turning out light.
2	Left	Left	
3	Right	Right	
4	Right	Right	
5	Right	Right	
6	Left	Left	
7	Left	Right	5 seconds after turning out light.
8	Right	Right	10 seconds after turning out light.
9	Left	Left	
10	Left	Left	
11	Right	Left	5 seconds after turning out light.

As will be seen by the later experiments reported in this paper, the chicks are probably as much stimulated by these rays as the human being. It is barely possible that the difference in the strain of chick used is responsible for the differences in our results. I think, however, that their method of allowing the chick to pick up grains of food illuminated by the different rays is a faulty one. In my experiments, where a large stimulating surface was used, the question of visual acuity does not enter in. It does unquestionably in their work. Furthermore, their work requires a reaction which runs counter to the chicks' ordinary habits. The birds in daily life constantly have occasion to pick up greenish-yellow grains, yellow grains, and reddish-yellow grains, but rarely or never blue and violet grains.

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*Hess, C. Untersuchungen über Lichtsinn und Farbensinn der Tagvogel. Archiv f. Augenkeilkunder, Bd. 57, S. 317.

†Katz und Révész. Experimentell-Psychologische Untersuchungen mit Huhner. Zeit. f. Psy., 1909, S. 93.

RELATIVE STIMULATING EFFECT OF MONOCHROMATIC LIGHT.

While at work upon the limits of the spectrum, it occurred to me that, since the chicks were already trained by this work on the extremes of the spectrum to respond to faint stimulation by light, it would be advisable to extend the scope of the experiment so as to obtain the curve of the relative stimulating effect of light of different wave-lengths. Such a curve has never been obtained hitherto on animals. It has been worked out for man under several sets of conditions—for the light-adapted eye, for the dark-adapted eye, and for eyes possessing various abnormalities in sensitivity to monochromatic light. This work, even on man, has been done in general with very poor physical controls. There is general agreement that the maximal sensitivity for the light-adapted eye lies in the region of the yellow-green, and for the dark-adapted eye in the bluish-green.

Furthermore, it is desirable to test the question whether the course of such a curve, when obtained in the chick, will be like that found in man. Comparison can be made only when the data for the two curves have been obtained under similar conditions.

Our procedure in obtaining the curves shown below was as follows: We first obtained refinement of the monochromatic light by the use of the auxiliary spectrometer (p. 88). Each monochromatic bundle before being admitted to the dark room was made to bear a standard amount of energy. The thresholds for the animals were then obtained by cutting down the energy of the light by means of the Brodhun sector. Since the different bundles worked with all have the same initial energy when admitted, the sensitivity curve can be plotted throughout the spectrum directly from the angular opening of the sector just sufficient to produce a response at the given wave-length, or as is more usual from the reciprocals of these values. In the curve these sector values are averaged for the three chicks.

The method of obtaining the chick's response was similar to that used in the work on limits. The apparatus was set for work at a given wave-length. The motor driving the Brodhun sector was started and left running during the whole course of the experiment. The intensity of the light falling on the stimulus patch was at first high (full 140 mm. of the Brodhun sector, but with the smoked glass in place). The chicks were given 10 minutes' complete darkness adaptation, then the tantalum light was turned up for 5 seconds, then came a wait of 5 seconds in complete darkness. The door to the reaction chamber was next raised and the chicks were allowed to respond. The stimulus on the first trial was always well above the threshold. On the second trial the angular opening was made considerably smaller; and on the succeeding trials, still further decreased, until at last a break-down occurred, *i. e.*, the chick refused to respond, or else waited long past the usual time for response, for adaptation to increase the stimulating effect of the light. I tried to regulate the steps so that a satisfactory value could be obtained and verified in the course of 12 to 16 trials. In several cases where doubt of the correct setting of the sector was possible, I delayed advancing on the following day to a new wave-length, in order to be able to repeat the experiments. It was not deemed advisable to use an ascending series of steps in this work, *i. e.*, to start below the threshold and gradually increase the intensity of the light until positive response was obtained (for fear of onset of position habits). If more time could have been given over to the experiment such a technique would unquestionably have been possible.

After the day's experiments upon the three chicks were over (the experiment lasted roughly an hour) my own threshold was taken. My wife adjusted the sector. The procedure was as follows: My eye was kept 1 meter from the plaster surface; the tantalum light was turned up for 5 seconds. While it was on I glanced at a neutral gray paper during the first 4 seconds (in order to avoid strong after-image). On the fifth count (metronome) I again fixated the plaster surface and shut my eyes while the light was turned out for 5 seconds. On the sixth second I opened my eyes and observed the plaster surface. If it were visible the experiment was repeated until the plaster surface was not visible immediately upon opening my eyes. This was repeated five times with ascending series and five times with descending series and the results were averaged.

Table 32 shows the actual sector openings for chick and man and the reciprocals of those values.

TABLE 32.

Wave-length.	In chick.		In man.	
	Sector opening.	Reciprocal.	Sector opening.	Reciprocal.
*660$\mu\mu$	870.00 mm.	.0011	900.00 mm.	.00111
600	10.72	.0932	7.36	.1358
580	9.90	.1010	2.82	.3546
550	1.52	.6578	.54	1.8518
520	1.40	.7142	.42	2.3809
480	1.98	.5050	.95	1.0526
452	2.66	.3759	1.82	.5494

The curve (fig. 10) is plotted from the reciprocals. It is clear that the higher the energy required for any given monochromatic light to stimulate the retina, the less the sensitivity of the retina to that light; that is, the reciprocals of the energy value ($1/e$, where e equals the energy necessary for stimulation) will, when plotted against the wave-length, give the usual form of a sensitivity curve.

In examining the curve it is well to remember that the higher the point on the curve is above the base line, the less is the energy required to produce stimulation. In this work we do not know in absolute terms (ergs) the standard energy carried by each beam with which we worked, but we do know that all beams had the same initial energy and consequently that the final sector opening at which the various thresholds were obtained are all directly comparable and proportional to the absolute energy required for stimulation.

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*The opening at 660 $\mu\mu$ is of course merely proportional. At all other wave-lengths a smoked wedge was used after the energy was calibrated, the transmission curve of which, from 396 $\mu\mu$ to 760 $\mu\mu$, was known (calibrated by Bureau of Standards). At 660 $\mu\mu$ the efficiency was so low that the wedge had to be removed.

The relative stimulating effect of the different regions of the spectrum for the (partially) dark-adapted eye appears clearly in the curve. The maximum efficiency for both chick and man is found at $\lambda = 5300$, which agrees fairly closely with what previous work we have upon man.* From the maximal point one finds a decrease in efficiency in passing toward either end. It is unfortunate that the calibrating of the selenium cell did not enable us to make tests with wave-lengths shorter than $\lambda = 4500$. The decrease in efficiency is enormous as one reaches the red. While in every region except red the curve of the human lies higher above the base-line than that of the birds, it is questionable whether the human has a lower absolute threshold than the chick. The method of obtaining the threshold of response for the chick here used was a rapid one. If more care had been taken and the absolute threshold had been desired, there is little room for doubt that the curve for the chick would more nearly coincide with that of man. I draw this conclusion from numerous chance experiments, some of which are cited in the text. A separate investigation for each wave-length would be required to thoroughly work out the absolute threshold values for chick and man. At $\lambda = 6600$ the present curve shows that the threshold of stimulation is lower in the chick than in man.

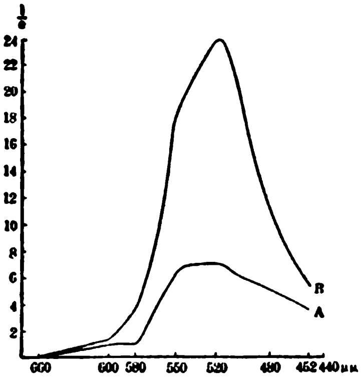

FIG. 10.—Sensitivity Curve (dark-adapted eye). A, chick; B, man. The ordinate shows the reciprocal (1 mm. = .01) of energy value necessary to produce reaction at the wave-length given on the abscissa.

RÉSUMÉ OF RESULTS OF STUDY ON CHICK.

(1) The limit of the chick's spectrum at the red end lies probably between $\lambda = 7000$ and $\lambda = 7150$; at the violet end between $\lambda = 3950$ and $\lambda = 4050$. The limits for the human eye have been found to lie between $\lambda = 4000$ and $\lambda = 7600$. These limits are flexible and depend somewhat on the absolute intensity of the light and necessarily upon the state of adaptation. Beyond these limits, visual responses are completely lacking. Unless the retinas of other day birds show sensitivity in the red far beyond the point at which response ceases in the chick, any theory to account for homing such as that of Duchâtel remains without scientific support.

(2) The curves for man and chick showing the relative stimulating effect of different regions are similar throughout their course, except in the extreme red.

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*See the work and historical summary of A. Pflüger, Annalen der Physik, 9 (1902), pp. 185–208. As will be seen, the curve obtained from the human subject here used shows only one maximum. In most of Pflüger's work there is evidence of a secondary maximum. While his work was apparently much more carefully controlled than my own, I am convinced that the secondary maximum obtained by him is due to some failure properly to control the energy of the stimulus

LIMITS OF SPECTRAL SENSITIVITY IN THE HOMING PIGEON.

At the time of completing the foregoing experiments upon the chick no homing pigeons of suitable age and stock could be found. In the fall of 1914 work was begun upon 4 young homing pigeons whose parents had "flight diplomas," but only one of them proved suitable for work. All were purchased when 3 weeks of age and were immediately given the preliminary exercises in the box shown on page 89. We experienced great difficulty in getting any of the pigeons to form the habit of passing completely around to the food. One pigeon, after several months of preliminary practice, during which tests were given daily, began to work steadily. By January 10, 1915, controlled experiments were begun. This bird was trained on yellow and green. It was found that while the pigeon was positive to light, it was not so automatic in its responses as the chick. After sufficient training, however, this pigeon became as invariable in its reactions to the light as the chicks. In the following account the tests on the intermediate parts of the spectrum are only summarized. As we approach the limits at the two ends the tests are given in detail.

LIMITS AT THE VIOLET END.

January 10. Eight tests on $\lambda = 5500$ were made. Only 1 error appeared.[*]

January 12. Eight tests on $\lambda = 5060$ were given, with no errors.

January 15. At wave-length $\lambda = 4780$: with slit in collimator open to 1 mm. and slit in objective open to 1.5 mm., the following tests were given, *without previously dark-adapting the pigeon* or allowing a period of adaptation after light was turned out (for method see p. 90). This test was made to get rapid orientation as to sensitivity of pigeon to light rays of short wave-length. The results were:

(1) Light on left side, wrong response.
(2) Light on left side, wrong response.
(3) Light on right side, right response.
(4) Light on left side, wrong response.
(5) Light on left side, wrong response.

Since a right position habit developed, I broke off the tests. It is evident that under the given conditions the light no longer controls the response. From this it would seem clear that there is no extreme sensitivity to violet rays.

January 16. Wave-length decreased to $\lambda = 4680$. *Animal was dark-adapted for 15 minutes,* and *30 seconds adaptation allowed before light was exposed.* Complete record as follows, with a result of 77+ per cent correct:

(1) Light on left, wrong response.
(2) Light on left, right response.
(3) Light on right, right response.
(4) Light on right, right response.
(5) Light on left, right response.
(6) Light on left, right response.
(7) Light on right, right response.
(8) Light on right, right response.
(9) Light on left, wrong response.

Under conditions of the above test it is evident that although the limit is not yet reached, the light has very low stimulating value.

January 17. Wave-length changed to $\lambda = 4580$; 15 minutes adaptation and 30 seconds adaptation before admitting light. 88+ per cent correct.

(1) Light on right, response right.
(2) Light on left, response right.
(3) Light on left, response right.
(4) Light on left, response right.
(5) Light on left, response right.
(6) Light on right, response wrong.
(7) Light on right, response right.
(8) Light on left, response right.
(9) Light on right, response right.

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[*] In all of the tests recorded here the purified spectrum of Helmholtz was used (p. 88). Unless otherwise noted, a Nernst glower burning at a constant amperage was used as a source. For general illumination (during feeding, etc.) a 40-watt tungsten was substituted for the tantalum light of the previous paper.

The responses were exceedingly rapid. The one error was probably caused by giving 4 tests on left side, and then changing.

January 18. By referring to the work on the chick it will be seen that the standard condition was 10 minutes dark adaptation and 5 seconds adaptation before exposing light. In the test below the slit in the collimator (S_1) was narrowed to 0.5 mm. and the slit in the objective (S_2) to 1 mm. Wave-length was changed to $\lambda = 4350$. Under these more difficult conditions the results were 28+ per cent correct.

(1) Light on left, response wrong.
(2) Light on left, response right.
(3) Light on right, response wrong.
(4) Light on right, response wrong.
(5) Light on left, response right.
(6) Light on right, response wrong.
(7) Light on right, response wrong.

Under such conditions the stimulating effect is not sufficient to control reactions. In this case the light was not visible to me, but it became visible when 17 seconds adaptation was allowed between turning out of light and exposure of stimulus.

January 19. Animal was again tested under same conditions, except that I waited before admitting animal until light became *clearly* visible to me. The seconds noted in first column give periods of adaptation before admitting animal. Results:

50 sec. Light on right, response right.
35 sec. Light on left, response right.
45 sec. Light on right, response right.
40 sec. Light on right, response wrong.
30 sec. Light on right, response right.
35 sec. Light on left, response right.
30 sec. Light on right, response wrong.
40 sec. Light on right, response wrong.
40 sec. Light on right, response wrong.

Since left position habit was setting in, I next widened slit in collimator to 1 mm. and allowed 60 seconds for adaptation. Light was visible to me at end of 10 seconds.

Light on right, response wrong.

I next opened slit in objective to 2 mm. (light visible to me at end of 4 seconds) and allowed 60 seconds adaptation.

Light on right, response right.
Light on right, response wrong.

It is evident that we are working here on threshold at the present intensity. Again the tests show clearly that there is no very great sensitivity to the violet—that the pigeon's retina is even less sensitive than the human retina to those rays.

January 20. I next tried the effect of greatly increasing the intensity of the light. The automatic B. & L. arc was used as a source instead of the Nernst: slit in collimator changed to 0.5 mm., slit in objective to 1 mm. The light so obtained was clearly over my threshold the moment it was exposed. Results:

(1) Light on right, response right.
(2) Light on right, response right.
(3) Light on left, response right.
(4) Light on left, response right.
(5) Light on right, response wrong.
(6) Light on right, response wrong.

Up to this point a 30 seconds adaptation period was given. Since the last two tests gave wrong responses, I increased adaptation to 60 seconds.

(7) Light on right, response right.
(8) Light on left, response right.
(9) Light on right, response right.
(10) Light on left, response right.

In this series it is clear that the limit of spectral sensibility has not yet been reached.

January 21. In order that we may readily reach the limits with the arc, I changed wave-length to λ = 4050, with all other conditions as in the test on January 19, except that the slit in the collimator was opened to 0.75 mm.

25 sec. Light on left, response right.
30 sec. Light on right, response right. Hesitated 20 sec. before starting.
27 sec. Light right, response wrong. Hesitated 15 sec.
40 sec. Light right, response wrong. Hesitated 15 sec.
40 sec. Light on left, response right. Evident that left position habit is forming.
30 sec. Light on right, response wrong.
55 sec. Light on right, response right.
35 sec. Light on left, response right. Hesitated 22 sec., then first went wrong and then turned to left.
30 sec. Light right, response wrong. Hesitated 25 sec.
33 sec. Light right, response wrong.
30 sec. Light left, response right.

On analysis it will be found that on all of the trials except two the bird went to the left side. As before, the first column shows the number of seconds required to bring the light *clearly* over my threshold. Since this was the greatest intensity of light which I could obtain with any purity, and since, further, the results seem reasonably clear, I decided not to make further tests on the violet region for fear of setting up a troublesome position habit (which would interfere with the work in the red region). The above tests show without further discussion that λ = 4050 under the given conditions is beyond the pigeon's limit of spectral sensitivity. Since the tests on January 19 show that at highest intensity λ = 4350 is not beyond the limits, it follows that the limit lies somewhere between λ = 4350 and λ = 4050. The pigeon is somewhat less sensitive to violet rays than is either man or chick. To completely work out this decrease in sensitivity in quantitative terms, while a fruitful problem, is beyond the scope of the present work.

LIMITS AT THE RED END.

January 22. In the tests on the sensitivity in the red region the Nernst was again used as the source. The slit in the collimator was set at 0.5 mm. and in the objective at 1 mm.; 10 minutes adaptation before beginning the tests was allowed and 10 seconds adaptation was allowed on each trial after the light was turned out before exposing stimulus light. Reading: λ = 6350.

(1) Color right, response right.
(2) Color right, response wrong.
(3) Color left, response right.
(4) Color right, response right.
(5) Color right, response right.
(6) Color left, response right.
(7) Color right, response right.
(8) Color right, response right.
(9) Color left, response right.
(10) Color left, response right.
(11) Color right, response right.

Has broken position habit carried over from violet. Animal hesitated at first and did not seem eager to work.

We thus see that changing directly from violet end, where left position habit was formed, to red end, resulted in the breaking of position habit. This confirms our results of the previous day in a striking way. The light now lying within the bird's range again controls the response.

January 23. λ = 6840; otherwise conditions same as above, except that slit in the collimator was opened to 1 mm. 63 per cent correct.

28* sec. Light right, response right.
18 sec. Light left, response wrong.
18 sec. Light left, response right.
20 sec. Light right, response wrong.
22 sec. Light right, response right.
18 sec. Light left, response right.
16 sec. Light left, response right.
20 sec. Light right, response wrong.
22 sec. Light right, response right.
20 sec. Light left, response right.
25 sec. Light left, response wrong.

---

*First column shows time required for the observer to see light. Stimulus light was then exposed to animal.

Under these conditions we find evidence that the light is exerting only a slight stimulating effect. While the responses are only 63 per cent correct, the fact that no pronounced position habit developed is the most significant evidence that the light lies within the animal's range.

January 24. I tried the pigeon on the same wave-length, but increased the intensity of the spectrum by using the arc light as a source. The slit in the collimator was closed to 0.5 mm. The light was over my threshold (with light-adapted eye) the moment it was exposed. Results:

Light left, response right.
Light right, response wrong.
Light right, response wrong.

In the above tests, since the light was so intense, I allowed only 10 seconds adaptation. Since a left position habit was forming, I increased the adaptation period to 30 seconds. 70 per cent correct.

Light right, response right.
Light left, response right.
Light right, response wrong.
Light right, response right.
Light right, response right.
Light right, response wrong.
Light left, response right.
Light right, response right.
Light left, response right.
Light right, response wrong.
Light right, response wrong.

Since there was a left-position tendency growing I decided to *retrain* on $\lambda = 5800$ (which was employed in the early training work).

January 25. Nernst lamp is the source. Slit in collimator 0.75 mm. Object of test, to see if position habit carried over to a situation where the stimulus was known to be effective. $\lambda = 5800$. Responses, 70 per cent correct.

Light right, response right.
Light left, response right.
Light right, response wrong.
Light right, response right.
Light right, response wrong.
Light right, response right.
Light right, response wrong.
Light right, response right.
Light right, response wrong.
Light left, response right.
Light right, response right.
Light right, response right.
Light left, response right.
Light right, response wrong.
Light right, response right.
Light right, response right.
Light right, response right.
Light right, response wrong.

This was an extremely difficult series in view of the fact that all but three trials were given on the right side. Even granting this, it is obvious that animal needs further training to remove position habit.

January 26. Conditions as above.

Light right, response right.
Light left, response right.
Light right, response wrong.
Light right, response right.
Light left, response wrong.

The last trial shows that left position habit has given way and that the large number of trials given on the right during the preceding day is tending to give a *right* position habit. From now on light alone should control response. That such is the case appears from the results of the remainder of the test, which gave 90 per cent correct.

Light right, response right.
Light right, response right.
Light left, response right.
Light right, response wrong.
Light right, response right.
Light left, response right.
Light right, response right.
Light right, response right.
Light left, response right.
Light left, response right.

The position habit has been corrected and the animal is once more automatic in its responses.

January 27. λ = 7120. Arc lamp; other conditions as on January 24. In to-day's series instead of again trying animal on λ = 6840, at which point a position habit began to appear, I gave light somewhat further along, λ = 7120.

After adjusting the intensity of the light so that I could see it (10 minutes adaptation) 20 seconds after tungsten light was turned off, the following results were obtained; 100 per cent correct:

Light left, response right.
Light right, response right.
Light left, response right.
Light right, response right.
Light left, response right.

In the above I had the slit in the collimator at 0.75 mm., which is too wide of course to give a very "pure" spectrum. I next narrowed this slit to 0.5 mm.

Light right, response right.
Light left, response wrong.
Light left, response right.

In the three trials last considered the animal began to wait from 1 to 3 minutes to respond. Fearing another breakdown, I again opened the slit to 0.75 mm.

Light right, response right.
Light left, response right.
Light right, response right.
Light right, response wrong.
Light right, response right.
Light left, response right.
Light left, response right.

There can be but little question of sensitivity here when the intensity is great. The breakdown at λ = 6848 was unquestionably due to the position habit. In the present series, the slit is so wide that it can not be determined whether the animal is reacting to the wave-length 7120 or to those slightly shorter which are undoubtedly present in the beam. It is hardly worth while to try to determine the limits any more accurately. The extreme red rays have little stimulating effect and the slits have to be opened wide in order to obtain a ray of sufficient intensity to call out response. Under such conditions we can no longer guarantee the purity of the light. One crucial test remains, however, viz, to give the animal the opportunity to react to rays beyond the (human) visible spectrum.

January 28. λ = 8000. Arc lamp as source. Collimator slit opened to 1 mm. and slit in objective to 1.25. The wave admitted ranged probably from 7700 to 8100. That the infra-red rays were falling upon the plaster surface was determined by the use of the selenium cell. No light was visible on plaster surface to me (or to Dr. Lashley) even after long darkness adaptation. Large deflections in the galvanometer were noticed whenever the selenium cell was brought in immediately above the plaster surface. One series of 10 trials was given. The order of the series was determined in advance by the throwing of a die. The results were as follows:

Light right, response wrong.
Light left, response right.
Light right, response wrong.
Light right, response wrong.
Light left, response right.
Light right, response wrong.
Light right, response wrong.
Light right, response wrong.
Light left, response right.
Light left, response right.

Again we see the onset of a pronounced position habit. The animal *went to left side on every trial, regardless of position of light.*

I then gave the animal immediately λ = 5700.

Light right, response wrong.

The position habit was carried over for this one trial, then gave way as follows, 100 per cent correct:

Light right, response right.
Light right, response right.
Light right, response right.
Light left, response right.
Light right, response right.
Light right, response right.
Light left, response right.
Light right, response right.
Light left, response right.
Light right, response right.

The results from all of the tests seem conclusive to the author. Somewhere in the neighborhood of $\lambda = 7120$, under the conditions of the present test, we find the limits of sensitivity. This is practically the limit we obtained for the chick (see p. 94).

RÉSUMÉ OF TESTS ON PIGEON.

(1) The range of spectral sensitivity in the homing pigeon lies approximately between $\lambda = 4200$ and $\lambda = 7120$. It was not our purpose to determine the limits with any great degree of exactness, since they are dependent to some extent upon adaptation and upon the absolute intensity of the ray of light exposed.

(2) The homing pigeon is not sensitive to infra-red rays, at least to those which have approximately a length of $\lambda = 8000$. Since neither a quartz nor a rock-salt prism was at our disposal we could not give an ultra-violet light of any intensity. The evidence on the violet end is clear, however, in view of the fact that the efficiency of the violet rays falls off apparently somewhat more rapidly for the pigeon than even for man.

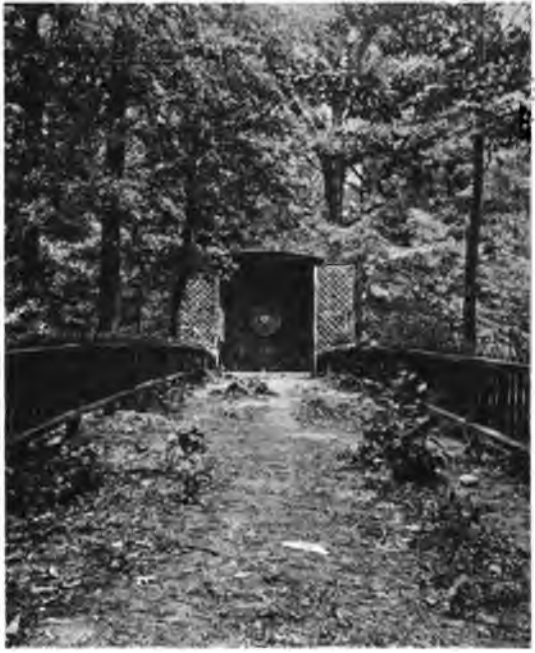
(3) Hess is unquestionably wrong when he states that the pigeon is "blind to blue and violet." We have shown the contrary quite clearly, even in the notes which we have presented in this paper. Our unpublished data show that this animal is sensitive to all wave-lengths between the limits expressed in (1) above.

(4) The young pigeon is positive to light, but is not so automatic in its responses as the young chick.

THE ACQUISITION OF SKILL IN ARCHERY.

By K. S. LASHLEY.

1



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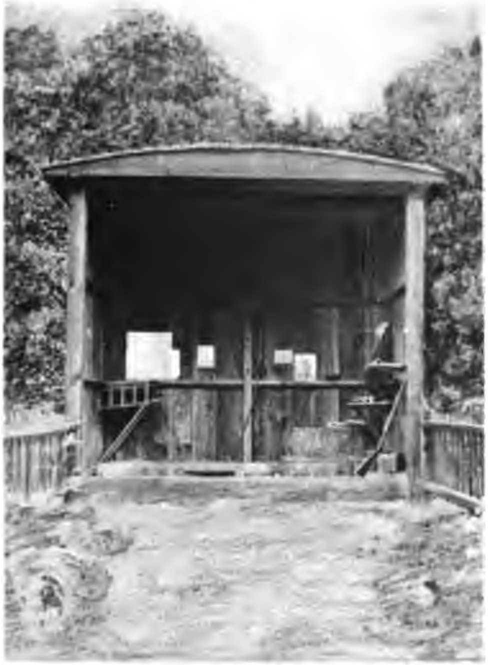

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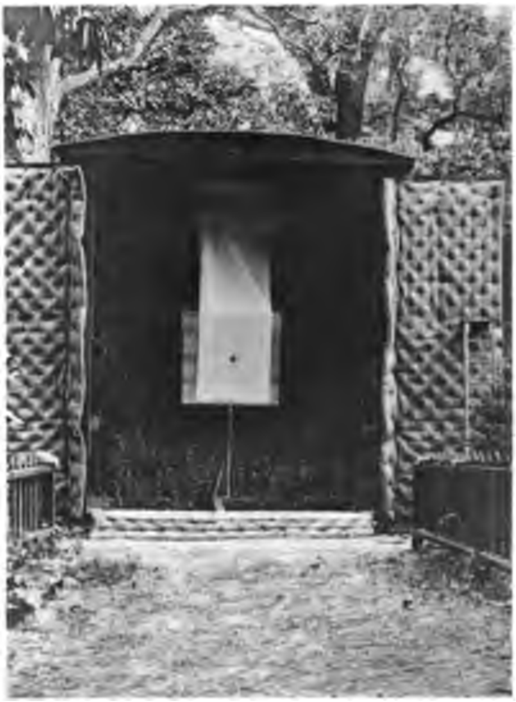

EQUIPMENT FOR ARCHERY.

Fig. 1. Homewood target as it appeared to the archers. Fig. 2. Practice shed with equipment. Fig. 3. Target arranged for rifle practice.

THE ACQUISITION OF SKILL IN ARCHERY.

The great majority of experiments upon habit formation in man have dealt with functions involved in implicit behavior; functions connected chiefly with the speech mechanisms have received most attention. Improvement in such activities as addition, translation into code or from code, solving mechanical puzzles, checking letters on a printed page, or memorizing word material is due almost wholly to increase in complexity of language habits. Practice in typewriting and musical technique is, in the beginning, followed by the formation of implicit* habits which later are dropped out to leave only the direct sensory-motor reactions from eye to fingers. Improvement in writing and in telegraphy probably involve similar changes. In the study of all such functions in human adults the subjects have already, at the beginning of the experiments, a vast number of constellations of habits in the implicit systems which have more or less in common with the problem offered by the experimental situation and may influence the course of learning in unknown ways. This is illustrated by the relation between the fullness of "meaning" of word material (*i. e.*, the number of habits in which the material is already involved) and the ease with which it is learned.

The existence of such complex systems of implicit behavior with their equally complex relations to overt activity makes it difficult to distinguish the different functions improved in learning, or to say whether a given amount of improvement is the result of a gradual coordination of many unrelated habits or of the simpler union of a few constellations of habits; whether the practice is distributed over a large number of nervous changes or is concentrated upon the fixation of a very few new neural pathways. For an insight into the mechanism of habit formation some simple, more direct sensory-motor associations must be studied, particularly such as permit of the control of related functions, metabolism, etc. This is best accomplished with animals, as they may be subjected to more vigorous training methods than is possible with man, but some types of learning in man, free from the complications of language habits, must be studied before the extension of the results obtained with animals to man will be completely justified. The activities studied by Bair (tossing shot), Whitley (tracing the smooth maze), Swift (tossing balls), Wells (tapping), and Partridge (inhibition of the winking reflex) call for the formation of relatively simple motor habits, but have the disadvantage of giving little to interest the subjects and probably offer a weaker stimulus to learning than is provided by more complex activities.

In the spring of 1913 Dr. J. B. Watson suggested archery as a means of studying habit formation in man which would in part avoid the complexity of language habits. Material for practice in archery was obtained and a preliminary experiment was begun by him at the Marine Biological Laboratory of the Carnegie Institution of Washington on Loggerhead Key, Tortugas. The chief object of this experiment was to test the value of the method and to work out the technique of experimentation, but the range of the experiment was extended to include a comparison of the rate of improvement in two groups of men differing in certain respects, to be considered later. The writer acted as subject and assisted in conducting this experiment. During the spring of 1914 the range described below was constructed on the grounds of The Johns Hopkins University and the experiments were continued in a study of the relation of the rate of improvement to the distribution of practice.

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*The term "implicit" is used in the sense defined by Watson (1914) as a common name for the movements, too slight for detection, which seem to bridge the gap between external stimulus and overt reactions when more than a single reflex is involved.

I wish to express my very great indebtedness to Professor Watson for the unrestricted use of the data obtained at the Tortugas, for the main features in the design of the apparatus employed in the later work, and particularly for his generous advice and assistance throughout the experiments.

My thanks are due also to Dr. Alfred G. Mayer for his interest in the work and for permitting his laboratory staff to devote their time to it.

Finally, I owe a great deal to the people who have taken part in the experiments, particularly to those in the "5-shot group," whose regular practice for many weeks was carried out at no small inconvenience to themselves.

EQUIPMENT.

The equipment used in the Tortugas experiments consisted of bows, arrows, target, screen to mark the results of wild shots, and a shield for the experimenter near the target. The arrows were of good quality, 28 inches in length. The bows were of lemon wood, 6 feet in length, and requiring a pull of 44 pounds to draw the arrows to the head. An arrow properly discharged from such a bow will pierce a half-inch pine board at a distance of 40 yards and has an almost flat trajectory for that distance. The target was the official 48-inch target of rye straw faced with white canvas, on which was painted a 10-inch black bulls-eye. It was mounted on a metal tripod so that the center of the bulls-eye was 4 feet from the ground.

The length of the range used in all the experiments was 40 yards, at which distance the bulls-eye subtends a visual angle of 33′. The target was set up at the foot of a sand-bank, which served to stop the arrows passing the target. As beginners rarely hit the target at this distance, some method of recording the distance of wild shots from the bulls-eye was necessary. For this purpose a muslin screen, 14 feet square, was erected around the target. The arrows made holes in the cloth and the distance from these to the center of the bulls-eye was taken as the record of the shots. This made it necessary to measure each shot as soon as it was fired, a method which proved neither convenient nor safe.

The method employed in the first experiment was the following: The subject was given instruction by word and example of the method of nocking, drawing, and loosing the arrow, but was told nothing of the method of aiming, the choice of a point of aim, or the general bodily position in aiming and loosing. He had to find out for himself how to aim, to prevent the bowstring from catching on his clothing or arm, to allow for the curve of the arrow's trajectory, to counteract the kick of the bow by increased tonus of the flexors of the left arm, together with the large number of finer details which make for accuracy. After the first instruction he was given a bow and 12 arrows and sent to a point 40 yards in front of the target, where he stood alone and loosed the arrows at intervals of 2 minutes, or in each case as soon as the preceding shot had been measured and recorded. Twelve shots were fired thus each day for 30 days. The subjects had no opportunity to observe each others' methods of shooting from a distance of less than 40 yards. Discussion of methods of shooting was prohibited, but not with perfect success. The result of each man's practice was posted daily and for group B (page 111) a prize of $5 was offered to the subject making the best score on the greatest number of days.

For the continuation of the work in Baltimore a safer and more convenient range was necessary. A plot of open ground, 40 yards in length by 8 in width, was laid out and the buildings shown in plate 8, figures 1, 2, and 3, were put up at opposite ends of this. The small shed (figure 2), which serves to protect and isolate the subject, is 12 feet high and 12 feet wide by 8 feet deep. It is equipped with racks for arrows, bows, etc., and a small telescope for use in rifle practice. The target shed is somewhat larger, 14 feet high by 12 by 12 feet (plate 8, figures 1 and 3). Three feet back from the open front of this shed is a pile of baled straw, packed tightly from the floor to the roof. The space behind this straw partition is used for the storage of extra equipment. The front of the shed is provided with large swinging doors, padded on the inside with heavy quilted canvas mats. When these are opened, as in the photographs, a surface 14 by 24 feet is exposed, which will catch and hold the arrows wherever they strike. The 4-foot straw target is mounted in the center of the baled straw and a 10-inch paper bulls-eye marks the center of this. Plate 8, figure 1, shows the appearance of the target-shed from the opposite end of the range.

In the main experiment rifle practice was used as an index of the relative ability of the subjects under the same conditions of practice. An efficient single-shot air-rifle was used at a range of 40 yards. The 4-foot steel-faced target used with this is shown in plate 8, figure 3. A constant supply of paper targets was provided, a separate one being used for each subject's daily practice. The entire equipment could be swung out of the way readily in preparation for arrow practice. As the bullet holes in the paper are not clearly visible at 40 yards it was necessary for the experimenter to watch the target through a telescope and report the position of each shot to the subjects.

COMPUTATION OF AVERAGES AND COMPARISON OF INDIVIDUAL AND GROUP RECORDS.

A series of records of shots with the bow or rifle invariably shows a great range in the accuracy of the shots, even in the case of subjects who have acquired a considerable degree of skill. With increasing skill the range of variation decreases, but the relative amount of variation as measured by the coefficient of variation remains practically constant. This is illustrated by the record of one subject given in table 33.

Some of this variation may be the result of the learning process itself (the successive trial of different methods), but the greater part of it is certainly due to chance external agents, such as variations in the strength of the wind, weight of the arrows, tightness of the nock on the string, tension of the bow, temperature, and extent of fatigue. As a result the average of any small number of shots does not give a fair measure of the skill of the individual, and the use of such averages as a measure of the initial and final accuracy and amount of improvement does not lead to trustworthy results.

In computing the relative progress of the groups it has been found necessary to omit the record of the writer as involving a different type of learning, and hence not fairly comparable with other records. Acting both as subject and as experimenter, the writer was forced to read such instructions on the use of the bow as were available, and to question the other subjects as to their methods of aiming and loosing. From this it followed that many of the adjustments which the others must make by the method of trial and error were reached by him directly through the mediation of preëxisting language habits. The advantage of this learning with instruction is shown in figure 13,

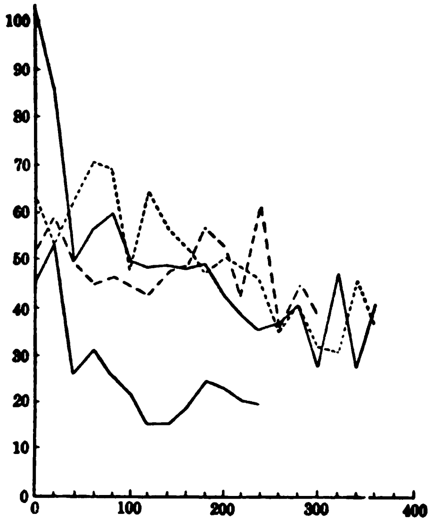


FIG. 13.—Rate of improvement with and without instruction. The heavy line is the learning curve of a subject who received detailed instructions. The lighter lines are typical curves of learning without instruction. Ordinates, distance from the bulls-eye in inches; abscissæ, successive shots arranged by twenties.

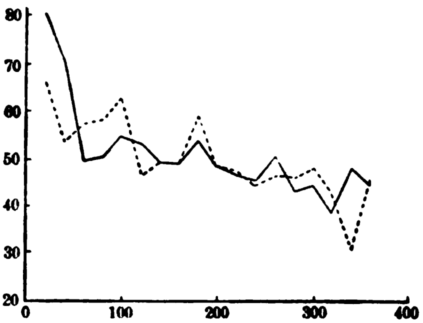


FIG. 14.—Learning curves of group A (........) and B (——) under light conditions of practice. ?

where the experimenter's record is compared with 3 other typical curves of learning without instruction. (In this figure, as in all the following learning curves, the ordinates represent the average distance from the bulls-eye of successive groups of 20 shots plotted on the abscissæ.)

TABLE 35.

	Group A.	Group B.
	inches.	*inches.*
1 to 180 shots	55.78	56.91
181 360 shots	44.80	45.77
Absolute improvement	10.98	11.14

The scores of the two groups, this one record being omitted, are given in table 36 and graphically in figure 14. If the averages of the first and last few shots are taken as indices of the total improvement, there is a fairly large difference in the amount of improvement shown by the two groups. The average, in inches from the bulls-eye, of the first and last 40 shots are given in table 34.

These averages make it appear that the laborers made the greatest absolute improvement, while the investigators showed the greater initial and final skill. From the appearance of the learning curves, it seems probable that the averages of the first and second halves of practice give the truer view of the skill and improvement of the two groups. These averages are given in table 35.

Table 36.—*Average distance from bulls-eye of successive groups of 20 shots, for two unlike groups of men under like conditions of practice with archery.*

Shots.	4 laborers.	3 investigators.	Shots.	4 laborers.	3 investigators.	Shots.	4 laborers.	3 investigators.
1 to 20	80.2	66.1	121 to 140	49.3	50.0	241 to 160	50.9	46.8
21 40	70.4	54.2	141 160	49.2	47.5	261 280	43.4	46.5
41 60	49.4	57.7	161 180	54.3	59.1	281 300	44.7	48.7
61 80	50.6	58.2	181 200	48.9	48.8	301 320	38.7	43.2
81 100	54.9	62.8	201 220	46.9	46.9	321 340	48.8	31.1
101 120	53.9	46.3	221 240	45.8	44.9	341 360	44.8	46.2

From this it appears that there is no significant difference, either in the absolute accuracy or amount of improvement shown by the two groups of men shooting under the same conditions.

DISTRIBUTION OF PRACTICE AND RATE OF LEARNING.

PURPOSE AND METHOD OF THE EXPERIMENT.

A year after the end of the experiment just described, with the completion of the Baltimore range, the work was taken up again in a test of the effect of the distribution of practice upon the rate of improvement. 26 subjects were distributed in 4 groups, shooting daily 5, 20, 40, and 60 arrows respectively. Owing to irregularity in attendance of some of the subjects, only 19 records complete to more than 300 shots were obtained, and this fact accounts largely for the differences in the number of subjects and composition of the different groups.

The method employed in the experiments carried out in Baltimore was not greatly different from that used in the Tortugas experiment. The subjects were given only as much instruction as seemed necessary to prevent accident. They were forbidden to discuss their methods of shooting or to seek outside instructions, and in his attempts to follow the various steps in the learning process the experimenter avoided, as much as possible, asking questions which might give the subjects a clue to better methods of shooting. In one respect the technique of the later experiment differed from that of the earlier. The subjects were practically all volunteers and so interested in each other's shooting that it was found impossible to prevent them from watching each other practice. This gave a considerable opportunity for imitation, which was not offered in the first experiment. The problem of imitation is considered on page 118. Rivalry between the various members of the groups was encouraged and the daily averages were posted on a bulletin board in the shooting-shed.

COMPARABILITY OF THE GROUPS STUDIED.

The subjects for the 5-, 20-, and 40-shot groups were boys and men ranging in age from 14 to 36 years. Those of about the same age were assigned to different groups, with the result that the average age of all the groups is approximately the same. Furthermore, from the data presented in figure 15, it seems clear that there is no correlation between the age of the individual and the rate of improvement of the function, and hence the slight difference in the average ages of the groups (a maximum of 3 years) may be safely disregarded.

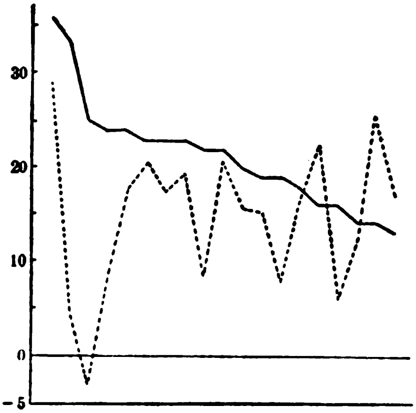


Fig. 15.—Relation of age to rate of improvement. Solid line represents ages of subjects in years arranged in order from left to right. Dotted line gives in inches the absolute amount of improvement for the subject in the corresponding position on the solid line. Averages are computed from first and last 40 shots.

The records of a woman are included in the averages of the 5-shot group. Analysis of the individual records shows that the averages of the group were not seriously influenced by the inclusion of this series of records.

With respect to previous training, none of the subjects had ever shot with the bow, beyond the sporadic practice with umbrella ribs and unfeathered arrows which comes within every boy's experience. In training in other functions there was a good bit of variation, but none of the subjects was particularly well trained in athletic sports or in difficult habits of manipulation, and, in general, the groups average out fairly well, with the exception of that whose members loosed 60 shots per day.

The study of the 60-shot group was undertaken after the others had finished shooting and after their average improvement had been computed. As it seemed that there was some advantage in favor of the 5-shot group, the attempt was made to test the effect of a still greater concentration of practice, continued until quite appreciable fatigue was produced. For this purpose the 60-shot group was organized, but since in the early part of practice this number is excessive, it was necessary to pick subjects who were physically able to meet the exactions of the experiment. As a result, the group was made up of young men ranging in age from 19 to 23 years, in better physical condition than the members of the other groups. The range of variation in age is less in this group than in the others, which fact probably gives an advantage to the group at the start. Furthermore, the superiority in physical strength of the members of this group gives an advantage quite aside from the question of fatigue, in that the bow may be drawn with greater ease and steadiness by an individual whose strength is not greatly taxed by its weight. Sixty shots represent about the limit that a beginner can shoot without rest during the first few days of practice, and it seemed that if fatigue had played an important part in determining the different rates of learning of the other groups, its effects should be much more marked in the records of the 60-shot group.

The averages of the Tortugas group, shooting 12 shots per day, have been included in the tables for comparison with the later groups, although these averages, like those of the 60-shot group, are not strictly comparable with the others. The average age of the group is considerably higher than that of the remainder, and the range, from 22 to 46, is likewise greater. The practice of the group was carried out under what seemed to be much more unfavorable conditions (at a temperature ranging as high as 110° F. and at times in a blinding glare of light, at others in a very strong wind which carried the arrows several feet from their direct course).

In all of the experiments enough arrows were provided to allow each subject to shoot his full daily number without pause. The arrows were marked individually and arranged in groups of 5, and the results of the shots were recorded by successive fives, as it was found to require too much time to keep all of the records in regular order. In the case of the 5-shot group the arrows were recorded in the order in which they were loosed.

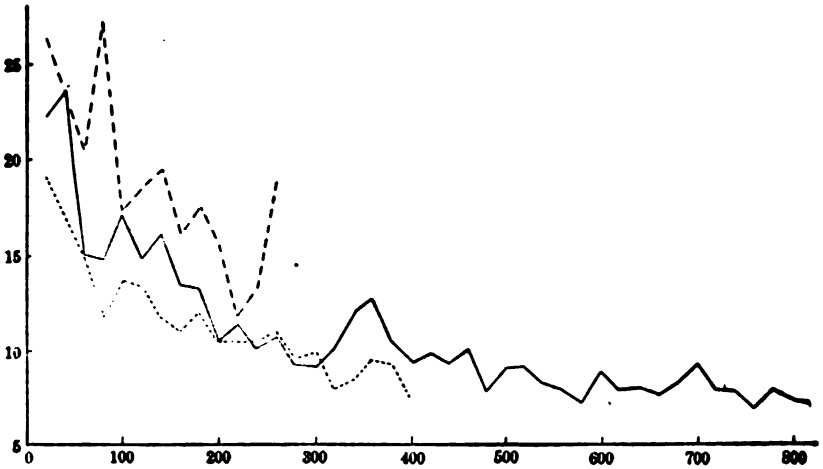


FIG. 16.—Learning with the rifle; all subjects shooting 20 shots daily. ——— 5 shot group; .... 20 shot group; ------ 40 shot group. Ordinates are distance from the bulls-eye in centimeters; abscissæ, successive shots averaged by twenties.

Finally, as a control upon the respective abilities of the groups to form habits of manipulation under like conditions of practice, each subject was required to shoot 20 shots daily with the rifle. The daily averages were computed and from these the average improvement of each group was obtained. Owing to the difficulty in securing subjects for the experiment, three individuals who had had some rifle practice were included. One of these was assigned to each group. Their records for rifle practice were not included in the group averages.

The daily rifle scores of the three groups are shown in figure 16. As in the case of practice in archery, it has seemed best to use the averages of the first and second halves of practice in judging the improvement rather than the records of the first and last few shots (see p. 110). The amount of improvement measured in this way is shown in table 37.

In so far as the improvement in rifle shooting may be considered an index of the relative ability of the groups, the 5- and 40-shot groups seem to be almost equal, the 20-shot group somewhat inferior in rate of improvement. When the percentage of improvement over initial accuracy is considered, as seems justifiable by the data given on page 111, the inferiority of the 20-shot group is less marked.

TABLE 37.—*Relative improvement of subjects shooting 20 shots daily with the rifle.*

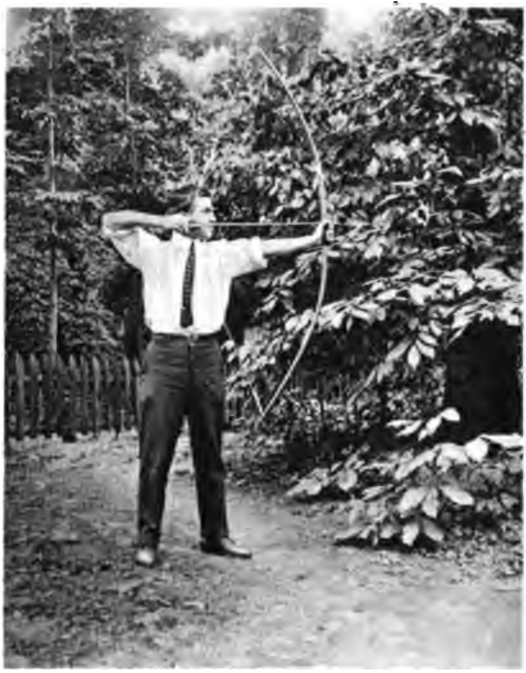
[The figures represent centimeters from the bulls-eye.]

Average of all shots.	Group shooting with the bow. (Shots daily.)		
	5	20	40
From 1 to 140	17.5	14.4	21.9
141 180	11.3	10.8	15.1
Absolute improvement	6.2	3.6	6.8
Percentage	35	28	31

CONDITIONS AFFECTING IMPROVEMENT.

Before comparing the relative abilities of the groups a few words are necessary concerning the complexity of the habits formed and the general character of the learning curve. Very delicate adjustments, both of the eye-hand coördinations at the moment of aiming and particularly in the quick changes in muscular tension at the moment of loosing, are necessary. The movements involved in loosing the arrow are the most difficult to control exactly. At the moment of aim the extensor muscles of the bow arm are resisting a pull of about 40 pounds; the flexors are under no strain. When the bowstring is released the extensors are suddenly freed from strain and tend to throw the arm outward. The tonus of the flexors must be increased immediately to counteract this tendency. The bow-arm of a beginner frequently swings 4 inches out of position before the arrow leaves the string and the delayed tensing of the flexors then draws it a still greater distance in the opposite direction. This movement must be almost wholly overcome before accurate shooting is possible. Equally accurate and difficult movements of the loosing hand must be acquired. An average variation of 2° of arc in the relative position of the hands results in an average of 25 inches from the center of the bulls-eye. Some of the championship records given below require an average variation of less than 30′ of arc in the alignment of the arrows.

The record of a subject whose practice extended to more than 1,300 shots is given in figure 17. This is the subject mentioned on page 122 as having had opportunity for practice of implicit habits before the beginning of the experiment. This accounts for the high initial skill and for the resulting flatness of the first half of the learning curve. With the exception of the high initial accuracy the curve seems to be typical for this amount of practice.



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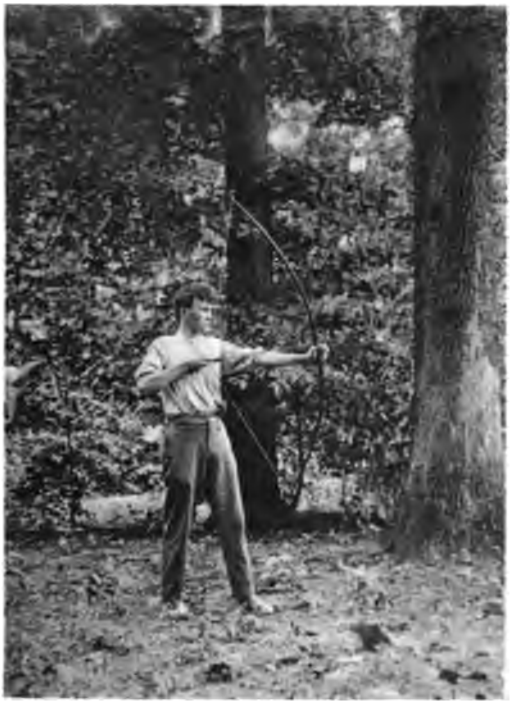

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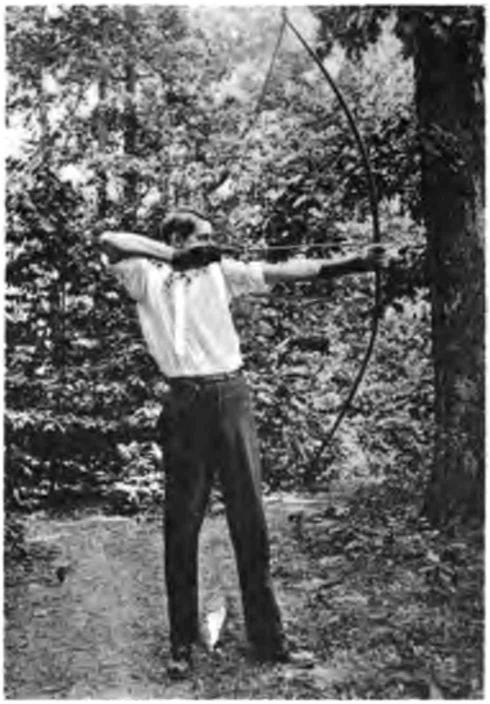

3

DIFFERENT METHODS OF AIMING.

Fig. 1. Sighting and kinæsthesia combined in aiming. Fig. 2. Aiming without sighting along the arrow.
Fig. 3. Position of the right hand determined by contact with the face.

Improvement after the average of 25 inches is very slow, with the suggestion of a plateau just before the quick improvement after 900 shots. Such periods of no improvement occur frequently in the practice curves. In some cases it has been possible to determine the cause of these with certainty. Thus one subject, after witnessing a slight accident occurring to another in loosing the bow, assumed, to avoid a repetition of the accident, an awkward aiming position and a slow release which interfered seriously with accurate shooting. The aiming position was quickly corrected, but the slow release persisted for many days and kept progress almost at a standstill. In general it seems that the plateaus are the result either of the accidental formation of conflicting habits, or that they represent points where no improvement can be made until a new method of shooting is hit upon by the method of trial and error.

The amount of practice recorded in the experiments was not sufficient to bring the skill of the subjects near the limit of improvement. The final accuracy of about 15 inches indicated in figure 17 is greater than that obtained by any of the other subjects. In comparison with championship records this average is still very high. The championship scores at the distance of 40 yards made in the double American round from 1880 to 1908 vary from 312 to 412. Reduced to inches from the center of the bulls-eye, they are about 11 and 7.8 respectively. The most consistently good record available is a practice score averaging about 5 inches for 90 shots. Studies of the rate of improvement from 15 to 10 inches are not available, but progress is certainly extremely slow. The writer, after reaching the average of 15 inches, has made scarcely any progress in 1,000 shots. The records used for comparison extend over only the first 360 shots, and deal therefore only with the preliminary stages of learning. During the first 100 shots, particularly, progress is made by leaps. The relation of the bow, hands, and arrow call out suddenly group habits of reaction to geometrical relations; the subject, for example, begins to nock the arrow at a constant place on the string and shows at once a marked improvement in accuracy. Most of the coördinations of larger groups of habits are formed very early in practice and probably account for the negative acceleration in the learning curves.

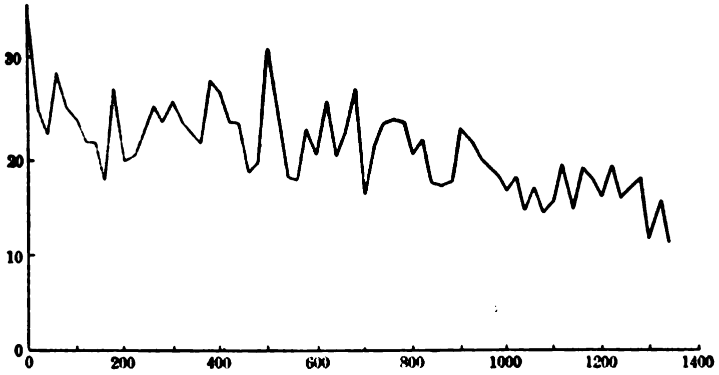

FIG. 17.—Improvement in long practice.

An attempt has been made to test the effect of fatigue upon the daily improvement. All first shots for daily practice were averaged for the 5-shot group. The second, third, etc., shots were averaged in the same way. The differences between the average of the first and fifth shots gives a rough measure of the improvement during practice. In the same way averages were obtained for the 20- and 40-shot groups, but the averages of successive 5 shots instead of single shots were taken, making the average improvement shown a little too small in comparison with that of the 5-shot group. These were then reduced to terms of average improvement during 5 shots loosed in rapid succession. The averages are 1.5 inches for the 5-shot group; 1.5 inches for the 20-shot group; and a negative improvement of 0.2 inch for the 40-shot group. The full data are given in table 38. Little more can be deduced from the results than that fatigue is much more severe after 40 shots than after 20, in the former case obscuring any progress made or perhaps preventing progress (see p. 126).

The question of improvement during periods of no practice is closely related to that of the effect of fatigue in obscuring the improvement during practice. The data have not been analysed carefully for the improvement during the 24-hour periods of rest, but the effects of some 48-hour periods of rest have been examined. In the 5-shot group there was a decided loss during these periods in the case of 3 of the 4 subjects. The fourth showed a slight gain. The absolute amount of gain was

+1.5 −5.0 −3.5 −3.2

With the results not obscured by fatigue there is a decided loss after practice is stopped.

For the 40-shot group the average gains during 48-hour periods without practice were

−0.5 −0.7 +2.5 +5.5

The record of the individual making the greatest progress during this period is given in figure 18. The solid lines of the figure connect the averages of the first and second 20 shots loosed daily. The dotted lines represent the intervals of no practice. The effects of fatigue are very pronounced in this case. Other individuals of this group show such effects to a less marked degree.

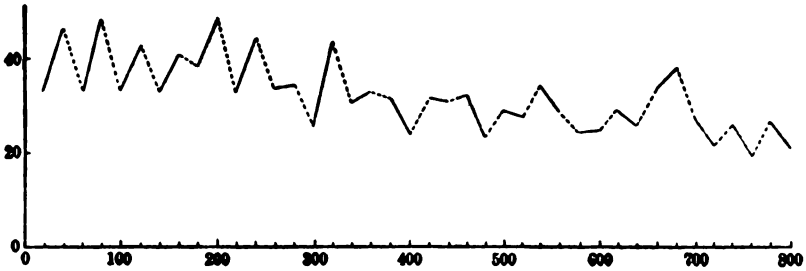

Fig. 18.—Effects of fatigue. Learning curve of one individual in 40-shot group is shown, plotted for successive groups of 20 shots. Solid lines show improvement during practice; dotted lines, improvement from one day to next.

The question of the part played by imitation in the improvement of the subjects is an interesting one. They watched each other's practice and the practice of the experimenter during the greater part of the experiment. From the different methods of aiming employed by different subjects it seems that imitation played no large part in the learning. Plate 9 shows the different methods of aiming which gave equally good results within the limit of practice. In the one case (figure 1) the alignment was obtained by sighting along the arrow, while the elevation was determined from the position of the right hand in terms of kinæsthesia; in other cases the subjects looked only at the bullseye and determined the relative positions of the hands almost wholly by kinæsthetic stimuli (figure 2). In the method of aiming shown in figure 3 the position of the right hand was determined by contact with the face, almost the whole adjustment being made in terms of visual and tactual stimuli. In the case of every subject some such peculiarities of aiming and loosing could be distinguished, and in most cases the aiming position could be traced out as the result of adjustment by trial and error to difficulties occurring in the early part of practice. Thus the position in figure 1 was assumed originally to prevent the arrow from falling off of the left hand when the bow was drawn.

TABLE 38.—*Effect of fatigue.*

		Average of successive shots in daily practice.					Average.
							inches.
5-shot group	1	32.7	38.7	24.2	26.4	....	30.5
	2	20.2	37.5	26.9	27.4	....	28.0
	3	28.9	35.4	28.8	25.3	....	29.6
	4	25.1	36.8	22.4	28.2	....	28.1
	5	22.7	43.2	24.9	25.1	....	29.0
Average improvement in 5 shots							1.5
		Average of successive groups of 5 shots in daily practice.					Average.
							inches.
20-shot group	5	26.9	44.4	50.2	50.2	48.5	55.5
	10	25.5	43.1	46.6	44.3	43.5	50.7
	15	23.3	41.4	46.3	47.5	45.1	50.9
	20	25.2	45.3	46.1	41.2	39.7	49.4
Average improvement in 5 shots							1.5+
		Average of successive groups of 5 shots in daily practice					Average.
							inches.
40-shot group	5	36.4	37.1	53.1	42.1	....	42.8
	10	30.8	31.0	54.1	50.2	....	41.5
	15	35.4	31.2	53.2	42.7	....	40.6
	20	29.0	31.1	48.5	46.4	....	38.7
	25	32.1	45.7	41.1	40.2	....	39.8
	30	31.3	41.6	54.6	45.1	....	43.2
	35	27.2	38.0	45.0	43.0	....	38.2
	40	31.4	46.1	50.8	49.5	....	44.4
Average improvement in 5 shots							−.2

The great opportunity offered in the experiment for imitation and the small extent to which it seems to have been used raises the question of the real value of imitation in human learning. It is hoped that the further use of archery will furnish more adequate evidence upon this point.

EFFECT OF THE DISTRIBUTION OF PRACTICE.

The group shooting 5 shots daily was organized first and their practice continued for about 2 weeks before the 20- and 40-shot groups started. Their practice extended, altogether, from June 22 until September 20. Practice could not be carried out on Sunday and comparable records of 360 shots were obtained from the 12 weeks' practice.

The 20- and 40-shot groups were organized at the same time and their practice was continued for 4 weeks, giving records of approximately 400 shots for each subject in the 20-shot group and 800 for each in the other group. Comparisons have been made only of the rate of improvement, measured in various ways, in the amount of practice represented by 360 shots. A more certain method of comparing the groups would have been perhaps to continue the practice of each group until a given degree of accuracy was attained and then comparing the amount of practice necessary to reach this stage, as was done by Ulrich in his study of the rat, but this method is practicable only when the final accuracy selected is near the limit of improvement, and the time requirements for such an experiment could not be met.

For purposes of comparison the records of the groups have been averaged in series of successive 20 shots and the curves in figure 19 have been plotted upon the basis of these averages, which are given in table 39. The daily averages are disregarded in this treatment of the data, which consist of averages for like amounts of practice. The records of the 12- and 60-shot groups are included for comparison with these others, although, as has been shown, these groups are not strictly comparable with the remainder.

TABLE 39.—*Averages of successive groups of 20 shots for the groups of subjects compared.*

[Figures are in inches from the center of the bulls-eye.]

Arrows loosed per day.					Arrows loosed per day.				
5	20	40	60	12	5	20	40	60	12
56.9	58.4	55.8	48.9	75.4	35.6	40.9	40.3	33.1	48.9
40.1	49.2	47.8	44.4	66.1	30.9	45.4	33.5	29.6	46.9
39.2	45.3	44.7	39.7	51.5	27.1	32.9	42.6	32.2	45.5
35.2	43.6	46.6	36.2	54.0	30.7	36.1	40.0	30.6	49.6
43.1	40.9	41.8	35.7	60.1	25.6	36.7	38.3	29.1	44.5
39.6	38.8	42.4	36.6	50.7	28.9	38.3	38.9	31.3	46.0
40.7	43.6	36.9	33.9	50.7	35.7	35.3	40.6	32.6	40.2
40.8	40.8	39.1	32.8	48.7	31.4	38.6	37.8	29.1	44.3
35.4	36.2	38.4	32.1	55.9	27.1	44.5	34.9	32.7	45.1

From inspection of the curves in figure 19 it appears that the 5-shot group is considerably superior to the others in final accuracy and in the amount of improvement, possibly excepting the 12-shot group. The superiority of this group is really somewhat greater than is apparent from the curve, for the sudden loss in accuracy coming at the 320th shot is the result of a few days of extremely cold weather, which stiffened the fingers of the subjects and made accurate shooting impossible.

The 60-shot group shows a greater average accuracy but less improvement than the 5-shot group. The 12-shot group shows a much lower accuracy than any of the other groups, with a somewhat greater amount of improvement. The improvement shown by the 12-shot group is in part spurious, owing to the method of recording the shots in this group. At the beginning of practice many arrows fell short. These were recorded as *failures*. In computing the averages these failures are counted all as 84 inches from the bulls-eye, which was, probably, an overestimate, and added something near 6 or 8 inches to the average records of the first 60 shots.

The amount of improvement in the 5 groups has been expressed in three ways: by the difference in average between the first and last 5 shots fired; between the first and last 40 shots; and by the differences in the averages of the first and last half of practice. These results are given in table 40.

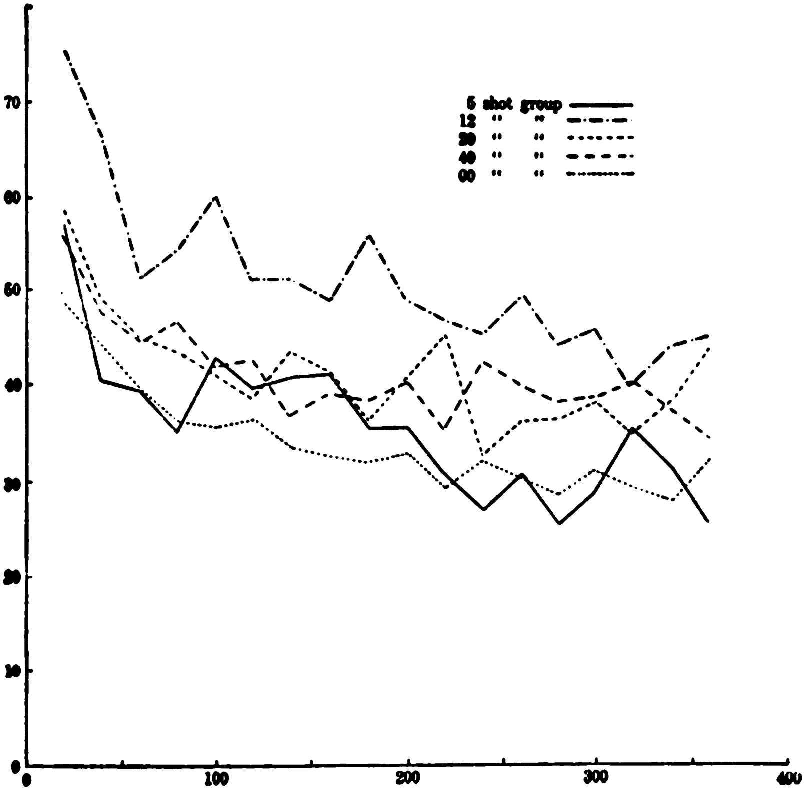

FIG. 19.—Learning curves for improvement in archery for 5 groups shooting 5, 12, 20, 40, and 60 shots daily. Arranged as in figure 13.

The absolute improvement, measured by any of these methods, is greatest in the 12- and 5-shot groups. The 60-shot group comes next with considerably less improvement, and the 20- and 40-shot groups are about equal. It appears from this that the rate of improvement per unit of practice is somewhat greater when the practice is distributed over many days than when it is concentrated into a few days. Whether there is a closer correspondence between the distribution of practice and the amount of improvement is not brought out by this method of treating the results, but an analysis of the data in a somewhat different way indicates that there is probably a fairly close correlation between distribution of practice and rate of improvement when chance causes of variation in the records can be eliminated.

During the first part of practice improvement is made largely by a series of what Thorndike has called "insights," such as those found so constantly by Ruger in the solution of mechanical puzzles. The sight and feel of the bow, arrow, and target present certain elements in common with the stimuli which call out many habits of manipulation and habits dealing with space relations and so tend to call out the same movements. Thus habits of aiming with the rifle are transferred to sighting along the arrow and need little modification to become efficient in producing accurate shooting with the bow. Such coördinations of complex preëxisting habits occur early in the practice of every subject, but whether they come before a single shot is fired, at the fifth shot, or at the sixtieth shot is largely a matter of chance. The subject whose record is shown in figure 17 had opportunity to see the practice of the 5-shot group for two weeks before his own practice was begun, with the result that many of the simpler problems of aiming were worked out in terms of the speech mechanism before he loosed a single shot. The result was somewhat the same as learning with instruction, as shown in figure 13.

Table 40.—*Improvement in accuracy after 360 shots with the bow.*
[Averages are in inches from the center of the bulls-eye.]

	Average of shots.				
	Group 5.	Group 12.	Group 20.	Group 40.	Group 60.
From 1 to 5.....	69.2	94.2	69.8	66.0	61.4
356 360.....	34.0	46.6	49.2	39.2	32.3
Improvement.	34.2	47.6	19.6	26.8	29.1
From 1 to 40.....	48.5	70.7	53.8	51.8	46.6
321 360.....	29.2	44.7	41.5	36.3	30.9
Improvement.	19.3	26.0	12.3	15.5	15.7
From 1 to 180.....	41.2	57.1	44.1	43.7	37.8
181 360.....	30.3	45.7	38.7	38.5	31.2
Improvement.	10.9	11.4	5.4	5.2	6.6

These factors result in a greater variability in the earlier part of practice than in later practice, which is independent of the distribution of practice, for few large groups of habits are added after the first 100 shots, as is evidenced by the fact that in later practice the subjects can rarely tell to what changes in their method of shooting their improvement is due, while in the early stages of practice such exclamations as "Oh, I've caught on to something," are frequently followed by sudden large increases in accuracy.

The elimination of the first trials, then, probably gives a truer picture of the effect of the distribution of practice than the inclusion of the earlier practice period. The averages of the first, second, and last third of practice have been computed for each group and are given in table 41.

As in all other methods of treating the data, practice with few shots per day seems to be more economical than that with many. In the first half of practice there is no close correspondence between the amount of improvement and the distribution of practice, but in the second half, where the effects of variations in the initial stage of learning are omitted, the correspondence is quite striking, the 60-shot group alone being out of order. The position of the 12-shot group, as inferior to the 5-shot group, is very probably correct, since in this case the error due to the overestimate of *failures* (p. 121) is no longer significant. The order of improvement per unit of practice is, then, 5, 12, 20, 60, and 40, with unrelated evidence to show that the 60-shot group was somewhat superior to the others.

To what extent do these results express the effect of the distribution of practice, and to what extent may they be due to chance? As has been stated, the 5-, 20-, and 40-shot groups seem very closely comparable in their make-up. The rifle practice, though not very dependable as an index to the abilities of the individuals, does give some indication that the relative rate of learning of the groups practicing under similar conditions is not the same as that obtained in the archery practice, which differed from the practice with the rifle only in its distribution, and thus that the differences in the rate of learning to shoot the bow are due primarily to differences in the distribution of practice. If the rifle records are to be trusted as an index to ability, it appears that the improvement of the 20-shot group should be counted as relatively somewhat greater than that of the 40-shot group, since the latter seems to show superiority in rate of learning under like conditions of practice.

Table 41.—*Improvement duing the first and second halves of practice.*

Average of shots.	Shots per day.				
	Group 5.	Group 12.	Group 20.	Group 40.	Group 60.
	inches.	*inches.*	*inches.*	*inches.*	*inches.*
From 1 to 120	42.35	59.60	46.03	46.53	40.25
121 240	35.08	49.40	39.96	38.47	32.29
241 360	29.90	44.95	38.25	38.42	30.90
Improvement:					
First half	7.27	10.20	6.07	8.06	7.96
Second half	5.18	4.45	1.71	.05	1.39

From the results of this experiment it is certain that practice distributed over many days is more economical than when concentrated to a few days. From the improvement shown in the later part of practice and general considerations of the relative abilities of the groups, it seems probable that there is a very close relation between the distribution of practice and the amount of improvement.

THE PROBLEM OF "DISTRIBUTION-RATE" RELATION.

These results agree very well with the general findings for the effect of the distribution of practice in the formation of other types of habits. Thorndike has summarized the more important work done before 1910, and it is unnecessary to review this work here in detail. In general, studies upon human learning indicate that the amount of improvement for a given amount of practice is directly proportional to the time interval between the practice periods and inversely proportional to the length of the practice periods, but there is some conflict in the results of experiments upon different types of habits. The results of a few experiments fail to show these relations, but do not seem to be conclusive.

For students learning to write English words in German script Leuba and Hyde give the results shown in table 42 for four groups practicing for periods of equal length but at different intervals. The group practicing every third day alone fails to show the advantage of distributed practice, and not enough subjects were used to eliminate the possibility that this is only a chance variation.

TABLE 42.

Group practicing.	Gained from fifth to tenth practice period.
	letters.
Twice a day......	240
Once a day.......	290
Once in 2 days....	395
Once in 3 days....	235

Lyon finds that short practice periods give better results in the formation of language habits, except in the case of short verse and prose selections whose meaning can be grasped as a unit; these are learned most readily by concentrated practice. In the case of such material, involving preëxisting language habits of almost inconceivable complexity, it seems very questionable whether the learning process is comparable to the formation of simpler habits.

Hahn and Thorndike found no advantage in favor of either of two distributions of practice, but their groups of subjects are not strictly comparable. The habits studied were those involved in computation and in every case the group with concentrated practice had the greater number of preëxisting habits, which may have obscured any disadvantages due to the concentration of practice.

With the exception of these cases the evidence favors the belief that the rate of learning varies inversely as the concentration of practice. The majority of investigators seem to believe that this holds true only within certain time limits, but with the possible exception of the results of Leuba and Hyde, no such limits have been established experimentally. The types of habits subject to the "distribution-rate" relation and the time-limits of the relation are not yet settled and the solution of the problem will demand a closer inquiry into the physiological causes of the relation than has yet been made.

The following quotation from Starch summarizes practically all the explanations which have been advanced to account for the effect of the distribution of practice upon the rate of learning:

> Why are shorter and more numerous periods economical? The main reason, no doubt, is the well-known fact that a period of rest after newly formed associations gives them a chance to become settled and fixed. The slower rate of improvement of the third and fourth groups is due in part to fatigue. The forty-minute group shows no gain in the last

period, and the two-hour group shows no improvement after the first hour. A third minor factor was that those working for a short period at a time were more apt to work with maximum concentration than those working for longer periods.

The majority of investigators have been content to ascribe the results obtained to "fatigue" or "interest," without attempting further analysis. In planning further experimental work the writer has found the following classified list of possible explanations helpful. It probably is not exhaustive, but may help to define the problem more accurately.

TRIAL AND ERROR.

A. Variety of Proprioceptive Stimuli.

When an organism is confronted with a new set of conditions its reaction is the summation effect of the elements of the external stimuli and the momentary proprioceptive stimuli. The latter may remain fairly constant during a single practice period, resulting in a rather stereotyped reaction. During the relatively long interval between practice periods the proprioceptive "set" may change and thus practice distributed over several days may offer the possibility of a greater variety of activities (some of which may lead to improvement) than the same practice confined to a period during which the same "set" persists.

B. Loss of Conflicting Habits.

W. F. Book has suggested that improvement during intervals without practice is due to the dropping out of habits which make for low efficiency and which have not had time to become well established, while the principal successful actions, more firmly established by longer practice, persist. Such evanescent habits, by restricting the variety of activities, may delay progress considerably and give a decided advantage to the interrupted practice.*

C. Change in the Primary Stimulus.

For successful learning by trial and error it is necessary that the organism perform diverse activities in response to a given set of stimuli. In experiments with animals such as those of Ulrich, the primary stimulus to this activity is furnished by hunger, pain stimuli, unfamiliar surroundings, etc.; in man by the many sublimations of instinctive reactions which constitute "interest," "fear of ridicule," "rivalry," etc. The number and variety of trial movements may depend upon the force of the primary stimulus, either as a result of the amount of diverse activity produced or of the concentration of the activity in responses to a limited number of stimuli, as when the hungry rat spends its time before the door of the problem box and is not distracted by the movements of other rats; or when the human subject keeps his attention strictly on the problem in hand. "Loss of interest through fatigue" probably represents a change in the intensity of the primary stimulus to activity.

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*The appearance and disappearance of habits of this type have been noted frequently during the experiment. For example, a subject assumes an incorrect aiming position in order to avoid catching the bowstring on his sleeve. This position persists for some time after the sleeve is rolled back out of the way, and may even become firmly fixed.

DIRECT EFFECTS OF FATIGUE.

Fatigue may have an effect upon the rate of learning in other ways than by changing the intensity of the primary stimulus.

A. Neurone Patterns.

It is probable that in order to obtain a given result different groups of neurones must be employed when the organism is fresh from those employed when it is fatigued. Thus, subjects in the 40- and 60-shot groups were seen to adopt different attitudes in aiming as they grew tired. The result of this is that a greater number of coördinations must be made to produce the same degree of skill whenever practice involves much fatigue.

B. Muscle Changes.

In archery there is a possibility that the effect of the distribution of practice is a function of muscle growth under different conditions of exercise. There seem to be no adequate studies on this subject.

PRACTICE BETWEEN PRACTICE PERIODS.

Where the subjects are interested in the experiment it is impossible to prevent their thinking and talking about it during the intervals between practice periods. This is the suggestion made by Thorndike in respect to Munn's results for language habits in substitution tests. It seems to apply equally well for the early stages of habits of manipulation in man (see p. 122), but its application to the rat in the maze test is questionable.

FIXATION OF THE NEURAL ARC.

Starch's first suggestion quoted above implies that a single activation of a neural arc starts up a process of fixation which continues for some time and that the further functioning of this arc during the process of fixation does not accelerate the process of fixation proportionately. By way of illustration, the following analogy may serve: Each time that a door with rusty spring hinges is opened it swings more easily. But when one man has opened the door others may follow him before it swings shut without wearing the hinges smooth. It is only when some time intervenes between the passage of the men that each reduces the friction in the hinge equally.

THE TIME RELATION OF PRACTICE TO THE CHANGES IN THE PRIMARY STIMULUS RESULTING FROM SUCCESSFUL ACTIVITIES.

The conception that the fixation of a habit is the consequence of its pleasurable result has been stated in a somewhat objective form by Ladd and Woodworth in a discussion of the escape of the animal from the problem box, as follows:

> We must assume in the animal an *adjustment* or determination of the psycho-physical mechanism toward a certain end. The animal desires, as we like to say, to get out and to reach the food. Whatever be his consciousness, his behavior shows that he is, as an organism, set in that direction. The adjustment persists till the motor reaction is consummated; it is the driving force in the unremitting efforts of the animal to attain the desired end. His reactions are, therefore, the joint result of the adjustment and of stimuli from various features of the cage. Each single reaction tends to become *associated* with the adjustment. But the unsuccessful reactions are less strongly associated than the successful, because each one of the former is at some moment given up or inhibited; and this inhibition, too, being

made under the influence of the adjustment, tends to become associated with it, and so to interfere with the association between the adjustment and the performance of this particular reaction. In the case of the successful reaction, however, the phase of inhibition does not occur and the only association with the adjustment is of the positive sort.

If habit fixation takes place in this way, progress perceptible to the subject should cause a quicker fixation of the habit. It is generally stated that long-practice groups can make an appreciable improvement in one practice period; that on this account their practice is more satisfying; and that this should result, therefore, in quicker learning. This would tend to produce a "distribution-rate" relation the reverse of that found.

In the present experiment the evidence makes it seem highly improbable that the "distribution-rate" relation was the result of differences in the primary stimulus. Members of the 5-shot group showed no greater interest in the problem than did the others; indeed, toward the end of practice, it seemed to the experimenter that the members of this group, after two months of faithful practice, were beginning to find the work something of a bore. The members of the 12-shot group were very busy with other work and seemed less interested in practice than any of the remaining groups. Yet these two groups made the greatest progress.

So far as the other possibilities are concerned, the present experiment offers little that is helpful in eliminating any of them. The effects of fatigue probably should not be emphasized too much. The 40- and 60-shot groups suffered far more from fatigue than did any of the others and their slower rate of progress does not seem proportionate to the amount of fatigue resulting from such long-continued practice. Changes in the muscles themselves, while possible in archery, are almost certainly precluded from language habits.

Which, if any single one, of the possibilities suggested is the real cause of the relation between the rate of learning and the distribution of practice, the evidence at hand is not sufficient to decide. Certainly some seem more, others less probable, but it is not certain that any of the four chief classes mentioned has been absolutely eliminated from any of the experiments thus far completed.

RÉSUMÉ OF RESULTS.

(1) The rate of learning to shoot with the bow was studied in two groups of men, one of the artisan, the other of the professional class. No significant difference in the rate of learning in the two groups was found.

(2) The rate of improvement of five fairly comparable groups during practice of the same function was tested under different conditions of practice. A close correspondence between the distribution of practice and the amount of improvement appeared, a given amount of practice being more efficient when distributed through many short periods than when concentrated in a few long ones.

(3) An attempt has been made to define the physiological problems involved in this "distribution-rate" relation.

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ALFRED G. MAYER, DIRECTOR

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I.

ON THE RHIZOCEPHALAN GENUS THOMPSONIA AND ITS RELATION TO THE EVOLUTION OF THE GROUP.

BY F. A. POTTS, M. A.,
Fellow of Trinity Hall and Balfour Student of the University of Cambridge, England.

Two plates and twelve text-figures.

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ON THE RHIZOCEPHALAN GENUS THOMPSONIA AND ITS RELATION TO THE EVOLUTION OF THE GROUP.

By F. A. Potts, M. A.

INTRODUCTION.*

The Rhizocephala are a group of undoubted Cirripedes having nevertheless a structure and life-history in which the departure from the normal type is probably greater than in any other parasitic Crustacea. They are found upon Decapod Crustacea and in the adult form have lost all trace of segmentation and appendages. Each one consists of an *external sac* communicating by a peduncle with an *internal root system* which traverses the body of the host and absorbs food from the blood. The absence of an alimentary canal and the development of an absorptive root system are characters which have been independently acquired in other parasitic crustacea, to wit, the Copepods *Herpyllobius* and *Rhizorhina,* which yet retain signs of segmentation and vestigial appendages. Moreover, in some parasitic Isopods (*Wanalia* and *Cryptoniscus*) and in the Cirripede *Anelasma* there is an incipient root system, although the gut does not degenerate. The modification of the reproductive phenomena is very considerable in the Rhizocephala, for it has involved the supression of the male sex and the conversion of the other into self-fertilising hermaphrodites or, in a few genera, parthenogenetic females.

The criterion of the Cirripede affinities of the Rhizocephala is to be found in the Nauplius and Cypris stages, which occur in their early larval history. Without the evidence of embryology it would be difficult to refer the adult even to the Crustacea. The external sac, in *Sacculina,* consists of a mantle surrounding a *visceral mass* but separated from it by the *mantle-cavity* or brood pouch (which opens to the exterior by a mantle opening) except along the surface of attachment to the host, where there is a communicating *mesentery.* A *nerve ganglion* and the small tubular *testes* lie in the mesentery; the main bulk of the visceral mass is occupied by the *ovaries* and there are present on each side an *oviduct* and a *vas deferens* opening into the *mantle cavity.* Geoffrey Smith (9), by comparing the arrangement of these organs with those of the typical Cirripede, has made a plausible attempt to homologise the external sac with the body of other Cirripedes. This brief summary of the typical Rhizocephalan structure is designed to show that, while structural reduction has proceeded far, it is by no means complete. But the retention of the mantle and the mantle cavity is due to the exigencies of the reproductive method in these forms, which compels an elaborate mechanism of ducts and incubatory spaces.

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*Service as a Lieutenant in the English Army has prevented Mr. Potts from revising the proofs of this paper.—A. G. M.

The most remarkable feature of the group, however, is the endoparasitic life-history, which has its only parallel in the Crustacea in the copepod family Monstrillidæ. The Nauplius and Cypris larvæ resemble those of other Cirripedes except in the absence of a gut. The latter fix at the base of hairs on the carapace of crabs and an internal mass of cells leaves the larval cuticle and passes through the gap in the carapace, which the articulation affords, into the body-cavity of the host. After a period of wandering it becomes attached to the intestine in the region of the abdomen and here it grows, absorbing nourishment from the blood and differentiating into a root system and a body destined to become the external sac. The internal stage of development is terminated by a moult in *Sacculina*, the sac-like body eating its way through the muscle and epithelium of the abdominal wall so that it emerges when the chitinous exoskeleton is cast. In adult life connection with the internal root system is maintained through the narrow peduncle occupying the aperture which served for escape.

Though it has been pointed out above that other parasitic Crustacea possess a root system, this is always developed, so far as is known, by a secondary inpushing of tissue from the externally situated body.

The complete description by Delage (2) of the development of *Sacculina* was published in 1884, but so extraordinary was its nature that for a long time doubt was cast upon the correctness of the account. In particular the late Alfred Giard maintained that the Cypris larva underwent metamorphosis into the adult at the precise position of fixation, as proved by his personal observation. It was not in fact until Geoffrey Smith, in 1906, published a striking confirmation of Delage's story that the matter was put beyond doubt. That an endoparasitic stage occurs in the life-history of *Sacculina* and *Peltogaster* is now certain; but it has not been actually proved to occur in any other genera of the group. For the most part they are similar in structure and habit and it may be safely assumed that their development runs through a course not unlike that of *Sacculina*. But, in one genus at least, *Thompsonia*, which forms the subject of this paper, the facts that an enormous number of external sacs are associated on the same host and that these sacs have an exceedingly simple structure seem to suggest that a different method of development may occur here. The endoparasitic stage must have been interpolated in the life-history and it is not perhaps unreasonable to suppose that amongst the many forms of the Rhizocephala one should be found to exhibit a simpler and, in its omission of the endoparisitic stage, more primitive life-history than that of *Sacculina*. Coutière (1), who has described the forms of this genus which infest Alpheids, under the name of *Thylacoplethus*, has reverted to the theory of Giard, supposing that each of the external sacs represents a Cypris larva which has fixed and metamorphosed in that identical position. The simple structure of the sac is another primitive feature, and we are led to believe that the more complex structure of *Sacculina* is due to progressive evolution from a form like *Thompsonia.* This view has also been taken by the few workers who have studied material of this Indo-Pacific form. The conclusions which are arrived at in this paper combat decisively the claim that the genus represents in any way the ancestor of the group Rhizocephala. As is so often the case, a form which seems at first sight to fill a gap between a group and its relations proves on closer examination but to illustrate an extraordinary capacity for specialised development in the group to which it belongs. But though the problem of *Thompsonia* thus changes with widening evidence, it is yet a form of great importance to the student of comparative anatomy and general biology.

PREVIOUS WORK ON THOMPSONIA.

In 1874 Kossmann (6) published a description of the Rhizocephalous Crustacea collected by Semper in the East Indies. In this class he placed a parasite, two examples of which were found on the walking legs of *Melia tessellata.* He named this animal *Thompsonia globosa,* the generic name being given in honour of that distinguished Irish naturalist who first recognised the Cirripede affinities of the Rhizocephala. The new genus was characterized by its globular shape and small size, long stalk with peculiarly thickened chitinous ring, absence of a mantle opening, reduction of the visceral mass, and retention of the larvæ until the Cypris stage was reached. Only two examples of the parasite occurred on this host, so the most striking feature of the genus, the presence of large numbers of external sacs of equal development, is not here recorded.

In 1902 Coutière (1) described a new type of Rhizocephalan parasitic on various Alpheids from East Indian and Australian waters and remarkable for the fact that each host carried under its abdomen, attached to the appendages, a great number of parasites, which resembled the eggs somewhat in volume and aspect. This parasite, for which he proposed the name of *Thylacoplethus* (several species of the genus were described) approaches *Thompsonia* in its form, but must, he says, be separated generically, first and foremost because its host, the shrimp *Alpheus,* is so different from the host of *Thompsonia,* which is the crab *Melia.* Besides, *Thylacoplethus* is distinct as the first example of a truly gregarious Rhizocephalan. I shall deal later with my own reasons for setting aside these conclusions of Coutière and treating the name *Thylacoplethus* as a synonym of *Thompsonia.*

The most interesting point in Coutière's papers is his daring supposition as to the significance of *Thylacoplethus* in the origin and evolution of the Rhizocephala. He remarks that the adult parasites exist on the pleopods in almost the very situation in which the attached larvæ of *Sacculina*[*] are found, and also that the root systems of adjacent parasites, if not entirely independent, are at any rate largely localised. These observations show that here at least infection of the host takes place by direct metamorphosis of the larva into the adult at the position of fixation, without the intervention of such a stage of internal parasitism as characterises the life-history of *Sacculina*. This conclusion points to *Thylacoplethus* as a primitive or even ancestral form and explains the "gregarious habit" as due to the simultaneous fixation of large numbers of larvæ.

The latest researches on *Thompsonia* have been made by Häfele (4) and Krüger (5) on material brought back by Professor Doflein of Munich from Japanese waters. The host in the larger number of cases was a species of *Pilumnus* (a Xanthid crab). Häfele was not able, owing to the absence of illustrations in Coutière's rather meagre descriptions, to decide whether his form was identical with *Thylacoplethus*[†] or not. But the possession by the latter of a distinct mantle and a cloacal opening led Häfele to suppose that the two forms might be safely placed in different genera.

In this paper the first attempt is made to give adequate figures of the parasite. Series of sections were cut to trace the course of the root system, but unfortunately a curious error of identification of the root tissue is made. This is corrected by Krüger from examination of material in the same collection. But both authors agree with Coutière in supposing that *each* of the external sacs is an individual formed by metamorphosis from a Cypris larva. Krüger alone seems to contemplate the existence of an internal stage in the life-history as a possibility.

In 1913 Dr. A. G. Mayer, Director of the Department of Marine Biology of the Carnegie Institution of Washington, kindly invited me to accompany the expedition of his department to Torres Straits. In arranging my programme for this purpose, it occurred to me that Coutière's observations were partly made on specimens from the very field of work to which we were journeying. I kept in view, then, the interest which an examination of fresh and specially fixed material of this form could not fail to possess, and was fortunate enough to procure specimens which throw a great deal of light on this obscure form.

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[*] In reality the larvæ of *Sacculina* do not fix more readily on the appendages than elsewhere.

[†] "La faible extension des racines, leur localisation dans les bourrelets saillant, dus à l'irritation causée par les parasites le grand nombre de ceux-ci, leur fixation dans une cupule deprimée de dehors en dedans, la presence de parasites adultes tres voisins sur les pleopodes d'*A. malleodigitatus*, ou de *Thompsonia* sur les pattes d'un Crabe la où s'effectuerait surtout l'inoculation des larves de Sacculine au stade Kentrogone; tous ces faits montrent que, ches *Thylacoplethus* au moins, l'infestation de l'hôte doit se faire par fixation directe des larves à leur place définitive, sans l'inoculation ni le stade de parasite interne qui paraissent caractériser l'évolution de *Sacculina carcini* Thompson."

PRELIMINARY DESCRIPTION OF MATERIAL.

During the first few days of our stay at Murray Island at the North end of the Great Barrier Reef, I sought for the Rhizocephalan parasite of *Alpheus* amongst the species dwelling in burrows on the reef (such as *A. edwardsi*), but without any success. On September 30, Dr. H. L. Clark brought to me a few specimens of a dark-coloured Alpheid (*Synalpheus brucei*, sp. n.), which he had found sheltering amongst the arms of a large Comatulid. One of these was distinguished from its fellows by the possession of numberless little pink egg-like* sacs attached to the thoracic legs and contrasting strongly with the purple colour of the cuticle of the host. These sacs were found to contain Cypris larvæ, and so little doubt remained that I was dealing with the creature described by Coutière under the name of *Thylacoplethus*. The next few days proved that, on the south reef of the island of Maër, there lived under every loose stone and within the branches of the living coral a teeming population of crinoids, of which the majority belonged to the species *Comanthus annulatum* (Bell). Within the living basket formed by the arms of the crinoid, a pair of Alpheids, male and female, were generally to be found, and a small proportion of the whole population were infected with the parasite. So numerous were the crinoids and their commensal Alpheids that they could be depended upon to provide a sufficient quantity of material for the study of the parasite. Only toward the edge of the reef, however, were the crinoids numerous, and as the spring tides waned it became more difficult to locate the crinoid with the water glass, to plunge beneath the water which covered its retreat, to extricate, by means of the brutal hammer or the persuasive hand, the unwilling echinoderm from amongst branching corals, to which it clung with desperate energy, and finally to prevent the escape of the agile Alpheid when the crinoid was raised above water. It was such experiences, however, which gave additional zest to our life at Murray Island.

I was eventually able to obtain nearly twenty Alpheids infected by *Thompsonia* in various stages of development. The external sacs varied from tiny bodies barely 0.5 mm. long to those a little more than 1 mm. in length and 0.6 mm. in breadth. In the latter stage the Cypris larvæ, with their dark eyes, could be plainly made out through the mantle. They were nearly always situated on the limbs. Some Alpheids only showed them on the abdominal swimmerets, where they were to be distinguished from the eggs of the host by their inferior size and different colour, but in the majority of hosts they occurred both on the abdominal and thoracic limbs. On some of the ambulatory limbs as many as a dozen were found, but in a late stage of development they were greatly crowded, as is shown in plate 1, figure 2. As

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*The eggs of the Alpheid are, however, green and are larger than the parasite.

recorded by Häfele,they are clustered thickly on the proximal part of the limb, while the last two or three joints are entirely free. Occasionally external sacs are found on the chelipeds and even the third pair of maxillipeds, though I have never seen them, as Häfele notes, on the eye-stalks of the host. Posteriorly they extend to the uropods and to both surfaces of the telson when the infection is heavy. Rarely, too, they spring from the pleura of the abdominal segments, but never from the terga and sterna.

On the last day of work at Murray Island (October 25) I obtained a swimming crab, *Thalamita prymna*, which was parasitised by another species of *Thompsonia* (pl. 1, fig. 3). The thoracic legs, including both the chelæ (text-figure 1), were thickly beset with elongated lemon-yellow sacs containing Cypris larvæ, much larger than those on *Synalpheus*. The sacs were nearly 3 mm. in length, counting the peduncle. It was impossible, as we were on the eve of departure, to obtain further material of this form, but the capture gave me an opportunity of examining the genus on its typical host, a Brachyuran. Since the swimming crab is much larger than the Alpheid, the number of external sacs is much greater on the former; a single ambulatory limb may have nearly a hundred external sacs upon it. Altogether there were certainly more than 500 on my specimen of *Thalamita*, while the number on *Synalpheus* never reaches 200.

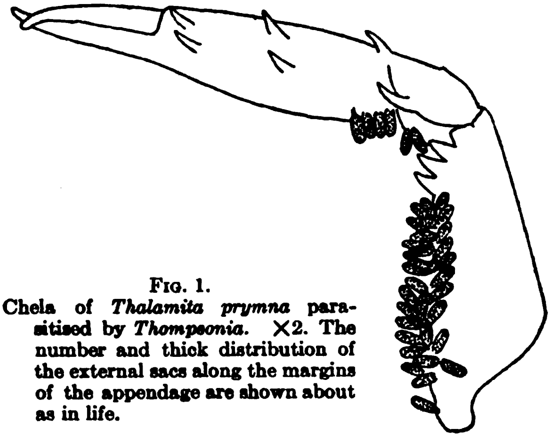

FIG. 1.
Chela of *Thalamita prymna* parasitised by *Thompsonia*. ×2. The number and thick distribution of the external sacs along the margins of the appendage are shown about as in life.

Dr. W. T. Calman, of the Natural History Department of the British Museum, has been kind enough to entrust to me a specimen of *Actæa ruppellii* (pl. 1, fig. 4) from South Africa, which also bears a large number of sacs of a species of *Thompsonia*. This species probably differs from that found on *Thalamita*, the sacs being much smaller and pear-shaped.

As far as I am able to judge, there is no essential difference between the forms of *Thompsonia* which infest Macrurous and Brachyurous

Decapod Crustacea respectively, although, owing to the scantiness of my material, I was unable to investigate thoroughly those of the latter class. The account which follows is based almost entirely on the parasite of *Synalpheus.*

THE ROOT SYSTEM.

The root system is the characteristic organ of the Rhizocephala. Delage and Geoffrey Smith have shown that it appears first in the course of endoparasitic development and is well established before the visceral mass begins to form. There is no doubt as to its existence and importance in all genera, with the exception of the doubtful form *Duplorbis*, but it has been exactly described only in *Sacculina.* The following brief description is condensed from the account of Delage:

> The tissue of the peduncle is bounded by the *basilar membrane* and from this the roots originate. For the most part they originate in a small number of large trunks which immediately ramify and spread. At first the roots follow the intestine, which they envelop with a close network. Some then pass into the distal part of the abdomen of the crab, penetrate the muscular layers of the body wall, and enter the abdominal appendages. Others pass forward and divide into two groups: the first follows the intestine and passes on to the stomach and into the interstices of the liver lobes and the genital glands; the second, not quite so important, accompanies the nerve chain, its branches following the lateral nerves into the limb muscles and penetrating into all the appendages, limbs, antennæ, and even the peduncles of the eyes. All the organs are invaded except the gills and heart.
>
> The roots branch with an irregular dichotomy. The separate branches never anastomose. In diameter they usually vary from 30 to 40μ, but the largest may measure 200μ. Histologically they consist of the following elements: (1) an exceedingly thin external layer of chitin; (2) a layer of cells forming a complete internal investment; (3) the interior of the root is occupied by star-shaped cells, the processes of which anastomose with each other and with the marginal cells. In the largest roots the centre is empty. Refringent drops or granules of yolk occupy the meshes. The root system of *Peltogaster*, though similar to that of *Sacculina* in details of histology and method of branching, has a very different distribution. It constitutes a compact mass which is concentrated in the neighbourhood of the peduncle, not invading the spaces between the tissues of the host in the manner characteristic of *Sacculina.*

Such accounts of the root system of *Thompsonia* as have been given by the earlier observers are conflicting and obviously influenced by a predisposition to accept the theory that each external sac is a metamorphosed larva. It is, moreover, exceedingly difficult to demonstrate the root system of Rhizocephala when preserved by usual methods, for the roots, owing to the impenetrability of their cuticular envelope, take up stains much less readily than the surrounding tissues. In addition, the highly refringent yolk globules, which make the roots easily distinguished in life, disappear under the action of alcohol or even formalin. And lastly, the roots are even more delicate than in *Sacculina,* so that we can well understand why Coutière and Häfele were unsuccessful in tracing the course of the system.

Coutière was nevertheless able to make out some details of their distribution. His description may be given in full:

> "Celles-ci s'ont bien différentes de ce que l'on remarque chez *Sacculina carcini* par exemple; elles sont même plus réduites que dans le genre *Sylon*, ou Hoeck les a décrites. Ces racines occupent uniquement le bourrelet transversal du pléosternites dont elles ont vraisemblablement provoqué la formation anomale; on n'en trouve nulle trace autour de l'intestin ni entre les muscles. Elles envahissent, par contre, les lames concentriques du neurilème externe, tres épaissi chez *A. edwardsi* et *A. avarus*. Elles ont un diametre de 25 μ a 30 μ et se montrent ramifiées et coutournées en tous sens."

Though Coutière is mistaken in supposing that the roots are localised in the neighbourhood of the sternum, his observations as to their absence round the intestine and concentration round the nerve cord agree with mine.

In *Pilumnus*, Häfele had a particularly unfavourable host for studying *Thompsonia*. The external sacs are all situated on appendages with an enormously thick cuticle. The only possible method of studying the root system was by prolonged treatment of the appendage in Perenyi's fluid to soften the chitin, after which sections could be cut. From an examination of these he concluded that there was a root system of an exceedingly simple kind. Krüger from a more careful examination of material from the same source, overstaining his sections and washing out carefully, was able to demonstrate a root system of a normal kind and show that the chromatin-rich nuclei which Häfele had taken to belong to the root system were actually in the connective tissue and blood cells of the host. The root system, then, Krüger decides, does not support the claim that *Thompsonia* is primitive, and, on the other hand, the omission of the Nauplius stage is a mark of specialisation. This is perfectly correct, and if he had suspected that the roots of adjacent sacs were continuous Krüger would have been able to complete his chain of reasoning.

My own conclusion is that there is a single root system continuous throughout the host, from which all external sacs are budded off so that each host is parasitised by a single individual and not by a hundred or more gregariously inclined Rhizocephalans.

I was first able to see the root system in the abdominal appendages of an infected *Synalpheus*. Those which bore external sacs were cut off from the living animal and examined under a low power of the microscope. The endopodites and exopodites are greatly flattened and the cuticle is thin and unpigmented. The whole organ is thus transparent and the roots are visible as slender strands to which the presence of innumerable highly refringent yolk granules gives a greyish colour. Usually a single root strand entered each ramus and this gave off a secondary root to each external sac and generally a number of others which ended in club-shaped swellings. The significance of these last will be explained later.

It thus became evident that the root systems of adjacent sacs at least were continuous, and since all the sacs upon one host are in the same stage of development, it was hardly to be doubted that the one system is common to all. Dissections of the trunks of infected Alpheids were made and carefully examined for roots. A perfect network of slender grey roots was seen to exist in the ventral body wall and to be concentrated particularly in the neighbourhood of the nerve cord.

The course of the root system in the body of the host particularly was best demonstrated, however, in preserved material. The infected animals were preserved for further study by fixing either with corrosive sublimate solution or Flemming's fluid. In those treated in the former manner the results are not very satisfactory. It is only possible to trace the roots because they take up stains so much more slowly than the surrounding tissue. In text-figure 2 an abdominal appendage is represented which bears a number of young external sacs. This was stained in a very dilute solution of borax-carmine for several days. The roots connecting the sacs are shown as colourless channels in the well-stained epithelial tissue of the appendage.

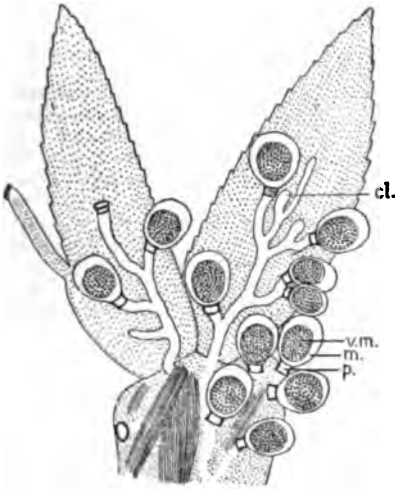

FIG. 2:—Abdominal appendage of *Synalpheus brucei* infected by *Thompsonia*; to show the branching root system connecting a number of very young external sacs. The specimen was fixed in corrosive sublimate and stained with borax-carmine. The roots have therefore taken up very little stain compared with the tissues of the host and are shown unshaded. *v.m.*, visceral mass; *m.*, mantle; *p.*, peduncle; *cl.*, internal bud of root system, which after further development will become an external sac. ×35.

But much clearer preparations were obtained from the individuals fixed in Flemming's fluid. In appendages from these mounted in Canada balsam without any further staining, the course of the roots is shown with the greatest clearness by the yolk granules, which are blackened by the osmic acid in the fixing fluid. The majority of the drawings which I reproduce here to illustrate the root system have been made from preparations of this kind.

The root system is not localised, then, in the neighbourhood of the external sacs; on the contrary, the main development is in the ventral body wall of the abdomen and often, too, the thorax, where it exists as a network of thin roots underneath and on both sides of the nerve cord, giving off frequent branches into the longitudinal musculature (see text-figure 3). In the thorax the roots extend into the lateral and dorsal body wall as well. Their distribution is not so wide as that of *Sacculina*, in that the intestine and stomach are not surrounded, but roots occur between the lobes of the liver. In the concentration of roots round the nerve cord rather than the alimentary system *Thompsonia* resembles *Mycetomorpha* (8), the root system of which has, however, a much more restricted distribution.

Branching is dichotomous and anastomosis of neighbouring divisions certainly does sometimes occur, a feature unknown in *Sacculina*.

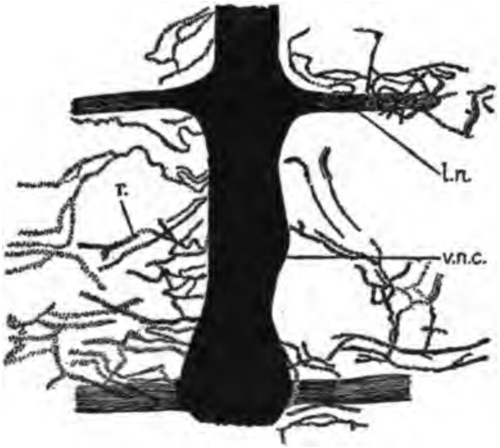

Fig. 3.—Root system of *Thompsonia* around the ventral nerve cord of *Synalpheus brucei*. It has been partially torn in removing from the body, and so the network is incomplete in places. Fixed in Flemming's fluid. The root system *r.*, here and in the figures which follow, is revealed by the blackened yolk globules which it contains. *v.n.c.*, ventral nerve cord; *l.n.*, lateral nerve. ×38.

This *central* or *internal* part of the root system is concerned, without doubt, with the *nutritive* function and is loaded with large and numerous yolk granules. From the trunk there pass out into the walking legs, abdominal swimmerets and tail-fans, lateral roots which, together with their branches, may be distinguished as the *peripheral* division of the system. It gives rise to the external sacs and its function is *reproductive*. The yolk granules, though numerous, are small.

In the case of the abdominal appendages a single root usually enters the protopodite, but it immediately divides and as a rule both the endopodite and the exopodite are invaded by secondary roots, which divide further, as mentioned above. Where the roots enter the abdominal appendages there is sometimes also an invasion of the space within the adjacent pleuron. Such a case is figured here (text-figure 4). A complicated knot of roots of the nutritive kind occupies the wider part of this space near the attachment of the muscles of the appendage and from this are given off two branches which pursue a tortuous course within the broad area of the pleuron. One of these branches has given rise to an external sac, of which the peduncle (*ped.*) alone is shown, but sacs occur only rarely in this position.

Similar wide extension of the system occurs when the tail fans and telson are penetrated, as is shown in text-figure 5. The single root whose course is followed divides into two, each of which gives rise to numerous short rootlets and finally anastomoses with its fellow. The rootlets usually end in club-shaped enlargements, but two have fully formed external sacs.

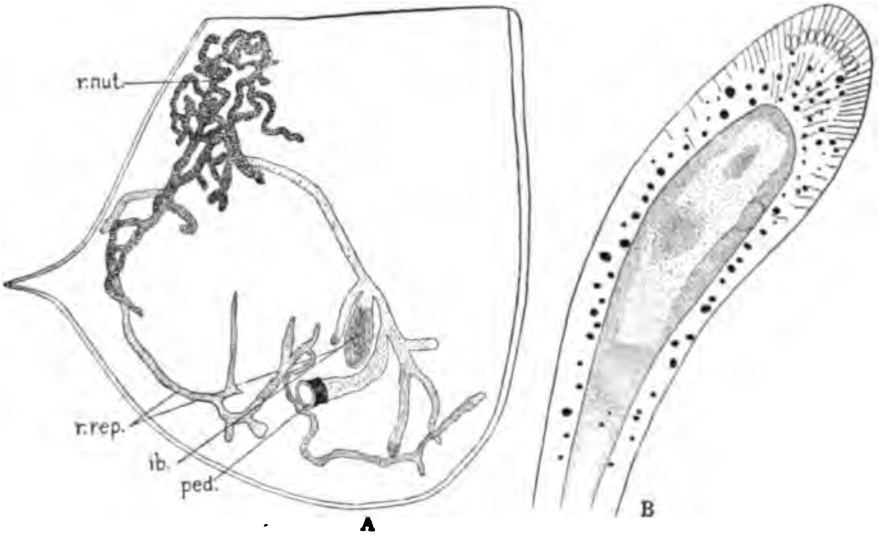

Fig. 4.

A. Pleuron of abdominal appendage of *Synalpheus brucei*, showing root system of *Thompsonia*. *r.nut.*, a number of roots like those of the interior of the trunk with large yolk globules; *r.rep.*, roots of the peripheral system with much smaller yolk globules. These give off one branch to an external sac, which, however, has been detached, leaving the peduncle, *ped.*, another process, *ib.*, which will shortly become an external sac, probably at the next moult, and numerous others which are not at all developed as yet. Fixed in Flemming's fluid. ×75.

B. Internal bud of *Thompsonia*. This is *ib.* of fig. A more highly magnified. ×450.

The histology of the internal roots (text-figure 6A) is similar to that described in *Sacculina*, with some modification perhaps due to the fact that they are thinner than those of the last-named form. In diameter they vary from 10 to 20 μ. There is a very thin cuticular investment covering a syncytial external layer, which contains a number of nuclei dispersed at irregular intervals. In the middle is a lacunar space, but I have not been able to demonstrate a lacunar tissue of stellate cells, such as is found in *Sacculina*. It is possible that this may be absent owing to the thinness of the roots. The large and numerous yolk globules are placed in the syncytial layer.

The roots of the peripheral part of the system (text-figure 6B) show two well-marked differences. The first of these I have already mentioned, namely, the smaller size of the yolk globules indicating that consumption rather than accumulation of food stores is the physiological condition in this region. The second is the occupation of the lacunar space by masses of small rounded nuclei with a scanty cytoplasmic investment. The external layer is, on the other hand, free from nuclei, which thus appear to have migrated internally. The origin of this lacunar tissue must be looked for in the external syncytium. Its function is undoubtedly reproductive; it accumulates particularly as the end of the rootlets which give rise to external sacs.

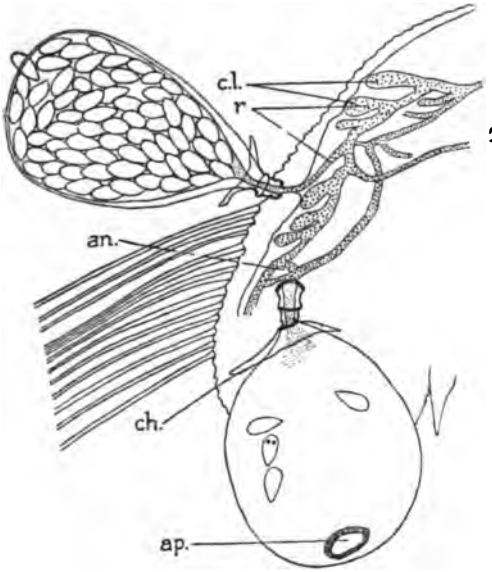

Fig. 5.
Thompsonia **parasitic on *Synalpheus brucei*, showing mature external sacs springing from a tail fan of the host. One is full of mature Cypris larvæ. In the other the larvæ have mostly escaped through the apical aperture, *ap*. The root system, *r*, is remarkable for the large number of internal buds, *cl.*, none of which are advanced in development. At *an.* anastomosis of two branches may be seen. The external sacs have recently undergone a moult and the remnant of the chitinous envelope, *ch.*, is seen around the peduncle. Fixed in Flemming's fluid. ×35.**

It will be well now to consider the terminal swellings of the rootlets (text-figure 4B). These are formed by the development of the external syncytial layer as well as the enlargement of the lacuna within. The external layer increases in thickness and the nuclei become much more numerous, migrating superficially, taking up a position with their long axes at right angles to the border. In fact, the tissue tends to assume a regular epithelial structure. Internally the protoplasm contains numerous yolk globules of various sizes and nuclei are rare and sparse. The interior lacuna is occupied by a dense mass of small rounded cellules of equal size which will give rise to the egg cells and nutritive cells of the external sac.

The whole structure is in fact a developing external sac. By the increase in size of the structure it comes into close contact with the chitinous cuticle, so that if the Alpheid were to moult it would emerge to the exterior. It is well known, of course, that *Sacculina* prevents its host from moulting. But some time ago I pointed out (7) that hermit crabs infected by *Peltogaster* still moult frequently and now it is to be recorded that, although the root system of *Thompsonia* is almost as extensive as that of *Sacculina* and the great number of external sacs must require a large and constant supply of nourishment, yet no check appears to be placed on the moulting function of the host. The number of moults observed was, it is true, only two or three, but this was due to the difficulty experienced in keeping *Synalpheus* in captivity and to the short time of observation, and I do not doubt that the moulting of infected specimens is a normal and frequent phenomenon.

Not only, then, is the whole number of existing external sacs budded off from one root system, but provision is made for replacing these when they have functioned. A necessary condition for securing this replacement is that the host should continue to moult. Further consideration will be given to the whole phenomenon after the sections dealing with the external sacs and the development of the egg cells. At present I wish to point out that the root system has the remarkable power of regenerating external sacs and producing germ cells throughout the whole period of its existence.

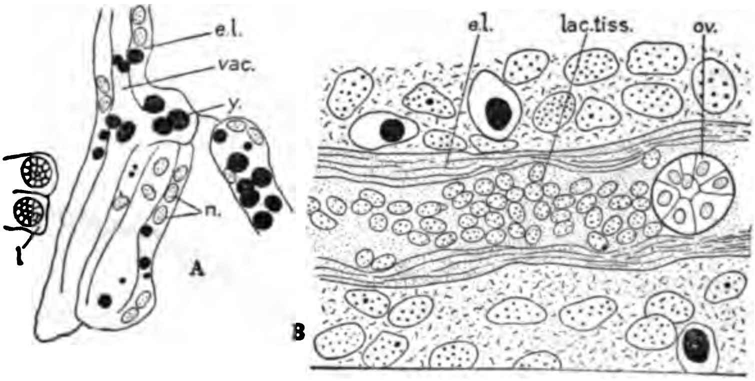

Fig. 6.

A. Roots of central system, showing external layer, *e. l.;* with nuclei, *n.;* lacunar space, *lac.;* yolk globules, *y.* ×660.

B. Root of peripheral system running through a pleuron of *Synalpheus*. This shows the non-nucleated external layer, the lacunar tissue, *lac. tiss.*, and a developing egg, *ov.* ×660. Fixed in corrosive sublimate and stained with borax-carmine.

If the distribution of the external sacs (which must follow that of the root system) is studied in a series of individuals it is seen to vary considerably. In some hosts they are confined to the abdominal swimmerets, but in the majority they are also present anteriorly on the thoracic limbs and posteriorly on the tail-fans and telson. In the former lightly infected individuals the root system has, we may suppose, been established for a comparatively short period, while in the latter class the root system has had time to spread throughout the whole body of the host. From the fact that the external sacs appear at first only on abdominal and never on thoracic appendages alone, we may safely conclude that the internal stage of *Thompsonia* fixes and grows in the abdomen of the host, as is the case in *Sacculina* and probably the other members of the Rhizocephala.

THE STRUCTURE OF THE EXTERNAL SACS.

It has already been pointed out that the external sacs are rounded or cylindrical bodies attached to the host by a peduncle and varying in length from 0.5 to 1.0 mm. in the parasite of *Synalpheus*, attaining to 3 mm. in that of *Thalamita*. The smaller forms are immature, the larger are occupied by larvæ ready to hatch. The external sacs are probably homologous with those of the typical Rhizocephala, but differ from this in the simplicity of their structure, a simplicity which is due to their large number and small size. Of the organs contained in the visceral mass of *Sacculina* or *Peltogaster*, the nerve ganglion, reproductive ducts, muscular tissue, and probably too the testis, have been lost.

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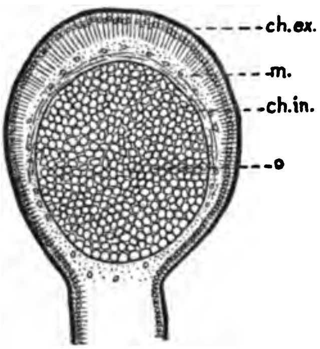

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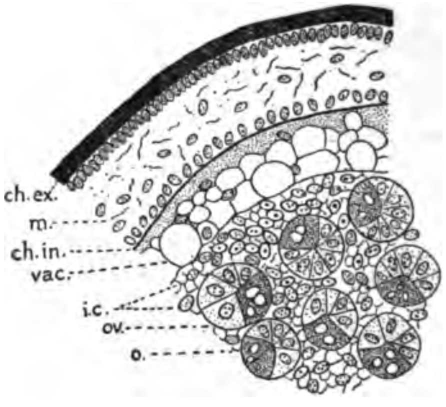

FIG. 7.—Young external sac of *Thompsonia;* whole preparation to show general appearance of mantle and ovary. ×60.

FIG. 8.—Portion of transverse section of a more advanced external sac. ×240. *m.*, mantle; *ch. ex.*, external layer of chitin; *ch. in.*, internal layer; *vac.*, vacuolated external layer of visceral mass; *o.*, ovary, with *ov.*, developing eggs, and *i.c.*, interstitial cells.

Coutière states that the external sacs of *Thylacoplethus* show the following typical Rhizocephalan structures: "Un *manteau* à double paroi, dans lequel est suspendue une *masse viscérale* et qui porte une ouverture cloacale." With this general summary I am in agreement. Häfele, on the other hand, does not appear to recognise any homology between the external layer of tissue (äussere Gewebeschicht) and the *mantle* of other Rhizocephala, or between the internal body (internale Gewebeschicht and Ovarium) and the *visceral mass*. There is, however, no definite *mantle cavity* between the mantle and the visceral mass, for the latter fills up all the internal space. The so-called mantle cavities which are described by Coutière and Häfele and figured by the latter author are, in my opinion, merely artifacts. In many of my own sections the shrinkage of the visceral mass due to unequal fixation has been followed by the appearance of a space between the former organ and the mantle, but in others the preservation is sufficiently good to show the true state of affairs. The thick external cuticle of the mantle prevents the proper penetration of reagents and on this account it is easy to make mistakes.

The *mantle* consists, in my material, of a syncytium in which the nuclei are mainly concentrated on the external and internal borders. This is due to the fact that there is secretion of chitin on these two surfaces forming an outer and inner investment of the mantle. The nuclei of the outer layer are more crowded and numerous in correlation with the greater thickness of the chitin here. The chitin of the internal boundary is exceedingly delicate, but it is only the presence of such a structure which enables us to homologise the outer part of the external sac with the mantle,* in the absence of a mantle cavity. Between the two thickly nucleated layers there is a mesh-work of protoplasm with a few scattered nuclei.

The visceral mass consists of an investing layer of vacuolated tissue with scattered nuclei (=innere Gewebeschicht of Häfele) which does not appear to take part in the secretion of the inner layer of chitin (*vac.*) and a central mass, densely packed with nuclei, in which the ova arise (*ov.*). This central mass was called the *ovary* by Häfele.

But distally to the ovary there is a second region where proliferation of nuclei takes place, but no egg cells arise. This is described by Häfele as a testis because the cells are rather similar to the spermatogonia of other Rhizocephala and many of them are in course of division. No spermatozoa are seen at any stage examined and an inspection of Häfele's figures does not inspire much confidence in his conclusion that *Thompsonia* is hermaphrodite. The active division of the nuclei in this region is accounted for by its apical position, which makes it a centre of proliferation. Growth proceeds throughout the development of the ova, until the larvæ are ready to hatch, and Häfele states that this organ has disappeared by that time. Certain large cells, with nuclei four to five times as great as those of the surrounding cells, seem to me to be clearly egg cells rather retarded in development, and their occurrence here shows that the apical portion of the visceral mass is not substantially different from the rest, but contains a larger amount of embryonic tissue.

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*The roots, mantle, and visceral mass of *Thompsonia* form a syncytium without any cell boundaries whatever, and it is not correct to speak of layers of cells, as Coutière and Häfele have done. This point is specially emphasised by Coutière.

So far as my own experience goes there is no sign of any organ which can be called a testis nor of spermatozoa wandering through the tissues. I think that probably *Thompsonia* is to be placed with *Sylon* and *Mycetomorpha* as Rhizocephala which have substituted parthenogenesis for hermaphroditism.

Coutière also seems to refer to this organ in speaking of a distally situated growing point. I must confess myself unable to understand a good deal of his description without the aid of figures. His conception of the life-history of *Thompsonia*, moreover, leads him to see in the visceral mass the abdomen of the Cypris larva and explain the proliferation here by the laws of growth observed in Annelids and Crustacean larvæ.

DEVELOPMENT.

The account which I give of the development of *Thompsonia* is very incomplete, for the material in my possession illustrates only a number of isolated stages. I have not been able to gather any information about the maturation of the egg.

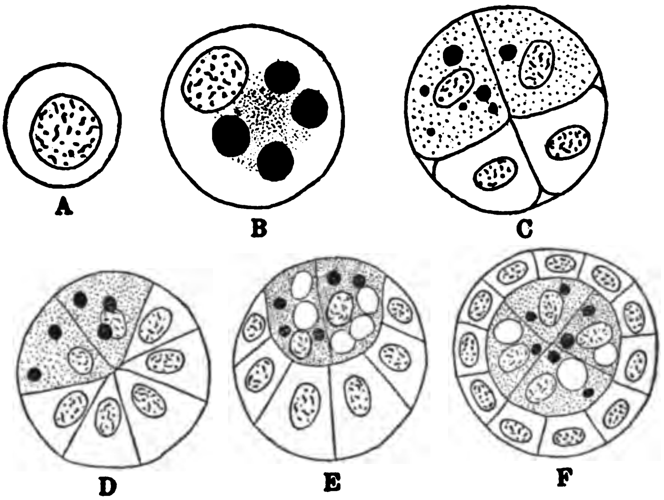

Fig. 9.—Developing eggs of *Thompsonia*. ×1000.

- A. Young egg cell.
- B. Oocyte nucleus has come to lie excentrically owing to the development of yolk (in black globules).
- C. Four-cell stage: two micromeres (unshaded) and two macromeres (shaded) containing the yolk.
- D. Beginning of gastrulation; micromeres have divided; macromeres undivided.
- E. Development of gastrulation; appearance of vacuoles in the protoplasm of the macromeres.
- F. Gastrulation complete; macromeres have divided once, so there are now four cells; more generally there seem to be three.

In the youngest external sacs the visceral mass is occupied by small cells of uniform size. Amongst these there soon become differentiated young oogonia which are rather larger than the remaining interstitial cells (text-figure 9A). These latter, when teased out from the living parasite, take up amœboid forms. In the oocyte stage the germ cells increase in size and yolk globules accumulate within them. In the internal buds this substance is confined to the external layer, but in the external sacs it occurs within both the visceral mass and mantle. The interstitial cells contain it and very possibly transfer it as required to the developing eggs.

When the oocyte attains its full size the nucleus lines on one side with the yolk granules occupying the largest part (text-figure 9B). They vary in number and are very unequal in size, but there are generally three or four large ones. The egg is very unlike that of *Sacculina* with its numerous equal-sized globules, which seem to occupy the whole space within the egg membrane. While, moreover, the egg of *Sacculina* is comparatively large, 600 to 800 μ in diameter, that of *Thompsonia* measures only about 34 μ.

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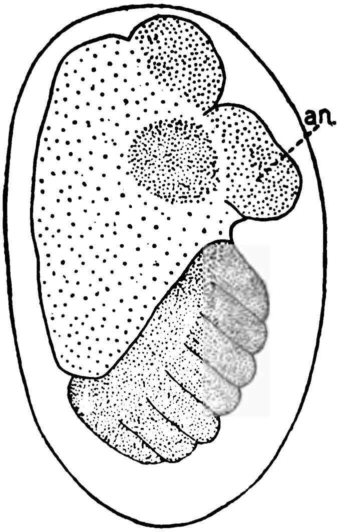

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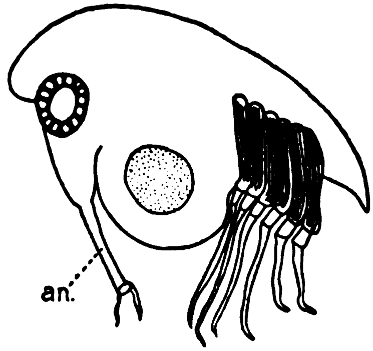

Fig. 10.—"Pro-Cypris" larva of *Thompsonia* from *Thalamita* in egg-membrane. ×375.
Fig. 11.—Cypris larva of *Thompsonia* from *Synalpheus*. The dotted area in the ventral part of the body contains reserve materials. *an.*, antenna. ×470.

Segmentation commences unequally, a micromere and a macromere with all the yolk being formed. Both micromere and macromere take part in the second (text-figure 9C) and probably also in the third division, but after this the yolk-containing cells cease to divide. The continued division of those without yolk leads to their rapid extension over the yolked cells and gastrulation (text-figure 9 D, E, F) thus takes place by epibole.

Beyond the gastrula I have not been able to trace development. The next stage observed is comparatively far advanced, showing a single pair of rudimentary processes, probably representing the antennæ. I am not able to say whether any stage resembling the Nauplius is passed through within the egg membranes, but think it is unlikely.

I figure here a "pro-Cypris" stage (text-figure 10) where the typical form of the Cypris has been attained, but the secretion of chitin has only just commenced and so the appendages have not assumed their articulate form. The embryonic antennæ are much larger in size than their ultimate development would lead one to expect.

The Cypris larva (text-figure 11) has rather a broad, squat form compared to that of other Rhizocephala. As Häfele has pointed out, it is very much reduced in organisation. The antennæ appear to lack the "appendices sensoriels," which in *Sacculina* are used for anchoring the larvæ to the hairs of the host. The distal article of the antenna is very small and the cement glands which might supply a secretion for fixation were not seen in the larvæ examined, so that it is not clear how attachment is effected in the first place. All these points in Häfele's description are borne out by my material. It is supposed by Häfele that attachment takes place on a freshly moulted crab, for the occurrence of external sacs on the hairless parts of the carapace must be explained in this way, according to the development in place theory; but since this theory is no longer tenable, we are left with the onus of explaining attachment in some other way. It is possible that cement glands are really present, but are seen only with difficulty in preserved material.

THE CHANGES IN THE VISCERAL MASS DURING DEVELOPMENT.

As development proceeds the larvæ take up more room, the egg membranes in which they are contained stretching with their growth. The interstitial cells appear to decrease in number and in the later stages the interior of the visceral mass consists of a mosaic of developing embryos, all in contact with small numbers of interstitial cells in the gaps between the egg shells. The mantle, too, as the result of the pressure of the embryos, becomes a very thin layer of tissue.

There is, however, a definite organ in the centre of the visceral mass which makes its appearance at this stage and retains its individuality until the larvæ hatch. This is a long thin process, the continuation of the peduncular tissue, and it is hardly to be doubted that its function is to supply nourishment to the developing eggs. (It is very well figured in Häfele, l. c., Taf. 2, Fig. 14, *schw.*) Coutière says, in reference to it, that it represents the whole visceral mass; he regards the developing eggs as now occupying the "mantle cavity" (cavitè incubatrice), while the ovarian epithelium has entirely disappeared. As stated above, the mantle cavity has no real existence in *Thompsonia*, and in young specimens it is not simply the matter of an ovarian epithelium, but the ovary occupies almost the whole of the visceral mass.

It is interesting, however, to compare this organ with the so-called "spadix" in the sporosacs of the Hydromedusæ. Here we have an exceedingly degenerate form of the medusa, with the germ cells lying between a single layer of ectodermal cells and the endodermal core. This latter is the "spadix" and it forms a tube which may be greatly elongated and even branched, wandering in the midst of the generative cells. In the general simplification of structure it is thus elaborated, no doubt, to supply nourishment to the developing eggs. But the organ described in *Thompsonia* is by no means so definite as this.

THE LIBERATION OF THE CYPRIS LARVÆ.

In Coutière's first note upon *Thylacoplethus* it is clearly stated that a cloacal aperture is present, which is, however, closed by "le paroi externe du manteau," by which I understand that the protoplasmic part of the mantle is penetrated by an aperture, but the chitinous envelope is entirely continuous. He believes that the embryos are liberated by a moult. Häfele, however, denies the existence of a cloacal aperture in the mantle of those species of *Thompsonia* which came under his notice. In *T. japonica* he states that the larvæ are finally freed by a longitudinal splitting of the chitinous envelope (l. c., Taf. 1, Fig. 1). But in a second unnamed species every external sac possesses a genital pore—that is, an opening in the chitinous envelope closed by a lid which falls away at the appropriate time. The agency of a moult is not required.

An investigation of my own material leads to conclusions in harmony with those of Coutière. In one example a number of the external sacs were more or less empty. All these had lost their chitinous envelope, save for a frayed collar round the peduncle. A small aperture was situated at the apex of the sac in the mantle and this gave a definite outlet for the embryos. This is represented in text-figure 5. The aperture must, however, make its appearance at a late phase of development; for, although it is such a regular and definite feature here, no signs of such an organ occur in any other specimens in my possession.

It seems likely that the description which Häfele gives of the larvæ of *T. japonica* escaping by means of an irregular rent in the chitin is an observation of an accidental case. With regard to the definite lid observed in another species, this may constitute a true specific distinction.

THE FORMATION OF NEW EXTERNAL SACS.

When the Cypris larvæ have all escaped nothing is left but a hollow sac (cf. text-figure 5). As the visceral mass thus disintegrates with the progress of the development of the larvæ, the question naturally arises whether the existence of the parasite is terminated at the birth of the first brood of larvæ. Häfele concluded that this was so.* But, as I have mentioned above, this question was answered in the opposite sense by observation of the moulting of an infected host. On September 30 an Alpheid was collected which bore large external sacs, containing Cypris larvæ, nearly all situated on the abdominal appendages. It was isolated and the next day was found to have moulted, the external sacs of course being carried away with the cast skin, which was preserved. Three days after this the host was examined to see whether any recurrence of external parasitic structures could be noted. A number of pink bodies much smaller than any observed hitherto, but with the characteristic structure of the external sac, were found on the abdominal appendages. One of these was cut off and, after being examined alive, was fixed carefully. I give here two figures comparing the old external sacs on the cast skin and the new on the appendage after moulting (text-figure 12); they show that the distribution is roughly similar, but in no case are the positions identical. The new

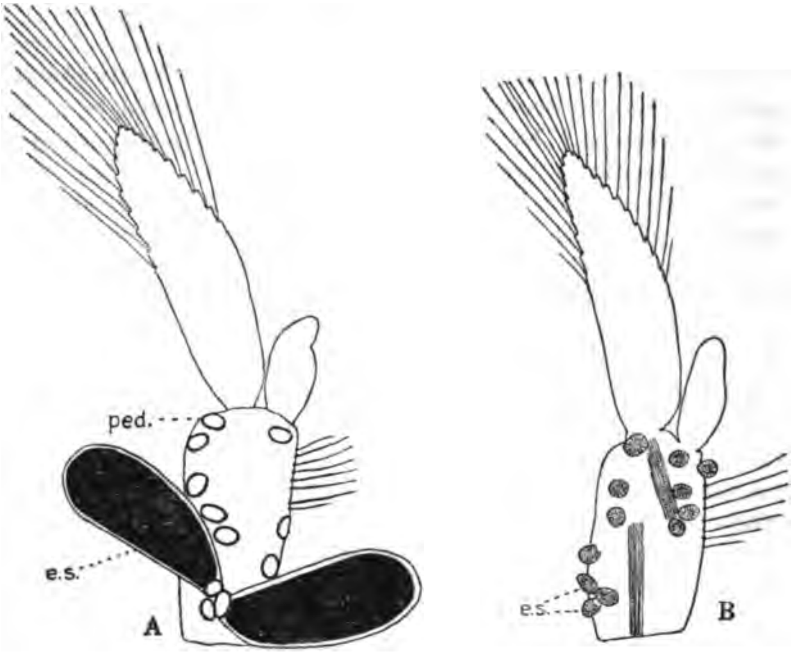

FIG. 12.—First abdominal appendage (right hand side) of *Synalpheus brucei* bearing external sacs of *Thompsonia*. ×28.

A. Cast skin showing external sacs (*e. s.*) containing nearly mature larvæ. Only two sacs are still present, the others having been accidentally detached, but the round black rings (*ped.*) indicate their position.

B. The same appendage 3 days after moulting, showing the new crop of external sacs.

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*"Diese Reduktion der Organe hängt offenbardamit zusammen, dass die Parasiten nur einmal fähig sind, Nachkömmen zu produzieren, wie aus den Verhalten des Ovariums und Hodens geschlossen werden kann."

sacs, then, evidently originate from the internal club-shaped processes of the root system; the rootlets which supplied the old external sacs do not regenerate new ones at once.

Clearly, then, successive crops of sacs containing the reproductive organs are produced by the root system. It would seem likely that the period of development of the parasite has been adjusted to correspond to the time elapsing between moults of the host. This theory is supported by the fact that in the case cited above the external sacs contained advanced larvæ at the time of moulting. I imagine that the disturbance connected with capture and change of conditions hastened the moult, which otherwise might not have occurred until the larvæ were liberated. If the correspondence does not exist, or is only partial, an immense waste must go on; for surely the moult of the host and consequent disconnection from the root system will suspend the development of the parasite and interfere with the mechanism for securing the liberation of the larvæ.

DEVELOPMENT OF GERM CELLS IN THE ROOT SYSTEM.

I have pointed out that the peripheral root system contains in its lacunar space multitudes of minute cells, which, in the formation of internal buds, migrate into the interior and form the ovary of the future external sac. At first they all appear exactly similar, but it is clear that only a small proportion actually become ova, the remainder being interstitial cells. We do not know how the germ cells are stimulated to simultaneous development, but whatever stimulus it is that so acts is not confined to the external sacs, but is also felt throughout the peripheral root system; for when this is examined in a specimen with well-developed external sacs there are seen, among the cellules of the lacunar space, much larger bodies corresponding in size and structure with the segmenting eggs found in the external sacs. One of these is figured here (text-figure 8, *ov.*). These eggs, for such they undoubtedly are, are not so numerous as those concentrated in the external sacs, but they are widely diffused throughout the peripheral system. They develop until gastrulation begins, but how much further than that I do not know. They certainly do not produce larvæ; yet the early segmentation seems to be normal and the egg is surrounded by a chitinous shell. In one of my preparations the egg appeared to break up at a later stage and the blastomeres to separate, but this was indicated only indistinctly. The existence of these bodies in the root system is exceedingly interesting and the problem of their fate is important.

I have not observed whether the stages of development of the eggs in the external sacs and in the root system correspond exactly.

THE SOCIAL FORMS OF PELTOGASTER AND THOMPSONIA COMPARED.

"*Peltogaster socialis* . . . is remarkable for the fact that it is never found solitary, but always infests a single host in numbers varying between 4 and 30, the usual number being about 20 . . . The numerous parasites affixed to each host are always at very much the same stage of development, so that the infection by so many individuals must have taken place at the same time. There is a certain mystery to be solved here, because the parasite in general is so rare that its occurrence, when it does occur in such large numbers on a single host, must either mean a most peculiar gregarious habit in the Cypris larvæ or else we must look for some quite different explanation. The explanation which occurred to me was that the numerous individuals on a single host are really the product of a single Cypris larva by a process of budding from the endoparasitic central tumour and its root system. Although this would mean an unique process in Crustacea, namely, the production of a true colony by budding, there is nothing inherently improbable in the hypothesis, if we take into account the peculiar nature of the development of the Rhizocephala, *i. e.*, the assumption in the middle of the developmental history of an embryonic condition.

"There is also a further fact which made me expect to find such a process of budding. Delage, in his memoir, makes mention (p. 665) of finding in the central tumour of a *Sacculina interna* two cellular masses, representing the future visceral mass and mantle, instead of one, and he wonders whether it is possible for a single tumour ever to give rise to two Sacculinæ; but he dismisses the idea partly because his preparation was a poor one and partly because this hypothesis is contrary to the general facts of development.

"Now, in the course of my investigations on *Sacculina interna*, I have found incontestable evidence on two occasions that Delage's first opinion is perfectly correct, and that occasionally two Sacculinæ may begin to form a single central tumour; but whether two such Sacculinæ ever come to maturity I am unable to say. One of these specimens is shown in plate 6, fig. 10. It is here seen that two mantle and visceral masses are developing opposite one another in a single central tumour, which must of course have been produced from a single Cypris larva.

"There is therefore a tendency towards a kind of polyembryony or budding of the 'nucleus' of the central tumour in *Sacculina*, and this led me to suspect that possibly in *Peltogaster socialis*, and in such a genus as *Thylacoplethus* (Coutière), in which the parasite is present to the number of about a hundred, this process of budding has become normal and permanent.

"According to this view it should be possible to prove that the root systems of the apparently separate individuals of *P. socialis* on the same host are all in connection; I was therefore at pains to investigate this subject. To my great disappointment I was able to prove that each individual has a separate root system at no point in continuity with that of another individual. Furthermore, in one instance I was so fortunate as to come across a crab infected with *Peltogaster socialis*, the individuals of which were still internal and at a very early stage in development, and even at this early stage there is no continuity between the tumours and root systems of separate individuals. Plate 6, fig. 9, is a section taken through two central tumours of *P. socialis* . . . The hypothesis, therefore, that the individuals of *P. socialis* are produced by budding from a single tumour receives no confirmation so far from the investigation of facts, but I do not yet altogether give up the hypothesis. It may well prove that the slitting up of a single central tumour into the rudiments of several individuals takes place at a still earlier stage, before any differentiation of the tumour has occurred, possibly soon after the entrance of the embryonic cells of the Cypris larva. The final test of this hypothesis must, however, be left to the future, for someone who has the opportunity of studying either this species or some such form as *Thylacoplethus*, where material is abundant."*

I have given this quotation from Smith in full because I feel certain of the general correctness of his suggestion that where "numerous individuals on a single host"† occur in the Rhizocephala they are really produced from a single Cypris larva by a process of budding. It is amply proved in *Thompsonia*, I claim, by the evidence here put forward, even though I have not been able to describe the endoparasitic stages; and in *Peltogaster socialis*, with which the passage I quote is specially concerned, I feel confident that a similar phenomenon takes place.

It is perfectly certain, however, that the details of the budding process differ in the two genera. Smith has shown in *P. socialis*, there are, in the endoparasitic stage, separate central tumours (the *anlagen* of the visceral mass) and separate root systems belonging to them. He suggests that division of the original embryo may even take place before there has been any differentiation. Thus early division and consequent development of separate embryos, each with a separate central tumour and root system, are probably characteristic of the budding process in *P. socialis*. In *Thompsonia* the parasitic organism is at all stages continuous within the body of the host and consists of a single root system which is established first, and a large number of reproductive sacs which are budded off and become external at a later phase. Their number and late and recurrent appearance are characteristic of *Thompsonia* and correlated with a degenerate structure.

It will be of interest in connection with this discussion to give a small series of drawings of a social Rhizocephalan very similar to *Peltogaster socialis* and, I think, identical with the form from Japan described by Krüger as a new genus and species (*Peltogasterella socialis*). In 1911, while enjoying the delightful hospitality of Professor Trevor Kincaid at the Puget Sound Marine Biological Laboratory at Friday Harbour, I collected a number of individuals of the hermit crab, *Pagurus alaskensis* heavily infected by this form. Plate 2 represents the parasite at three widely different periods of growth, but in each case all the individuals are of uniform size, and, it can hardly be doubted, of the same age too. The only alternative to a theory of budding is that of simultaneous fixation of the Cypris larvæ. This theory indeed supposes, as Smith remarks, "a most peculiar gregarious habit in the larvæ," and when we remember that marine larvæ are dependent for distribution, so far as we know, on chance vagaries of current rather than an internal migratory instinct, I for one can not suppose that so many larvæ should share a common path to their intended host and achieve such remarkable success in fixation. It is true that Delage, experimenting on the development of *Sacculina*, found that of a brood of Cypris larvæ, confined in a small aquarium in company with a crab, large numbers were found attached to the carapace of the crab; but this was certainly due to the stillness of the water in the aquarium and the small space in which the thousands of larvæ were confined, conditions which would hardly be repeated in nature. The fact that two Sacculinæ are occasionally, and even three rarely, found on a single host shows that contemporaneous infection does take place, but it also shows, I think, its comparative infrequency.

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*Smith, l. c., pp. 57–58.

†This does not apply to all the numerous instances where a crab bears two or three *Sacculinæ* or a hermit crab more than one *Peltogaster*. Far more commonly these must be cases of successive infections.

I regret that I can not throw further light on the question of the continuity of the root systems of adjacent parasites, for I think Geoffrey Smith's statement requires confirmation. The time at my disposal was short and material came into my hands only early in my visit, so I did not preserve it carefully for histological study. Nor was I able either to make the search I had intended for the *Peltogaster interna* stage. But the whole life history is worthy of an exhaustive study by some worker on the Pacific coast having access to this rich source of material.

THE EVOLUTION OF THOMPSONIA.

If a budding process is actually proved to exist in *Peltogaster* and *Peltogasterella* it helps us to understand how such a form as *Thompsonia* has risen. When once the continuity of the root system in *Thompsonia* is demonstrated, it becomes impossible to regard it as a primitive representative of the group; it must, on the other hand, be admitted to be the most specialised of all. The root system is undoubtedly a new development unrepresented in the typical Cirripede; but in the course of endoparasitic development in *Sacculina* it appears before the central tumour, which in its complete development as external sac may still be said to show something of Cirripede structure. But the retardation of the appearance of the external sacs here foreshadowed reaches its climax in *Thompsonia*. There is here still further exaltation of the root system at their expense, for not only do the roots fulfil their nutritive functions, but they also produce germ cells. The root system is, in point of fact, the organism and the external sacs are merely externally placed ovaries, organs of a wholly transient nature.

It is hardly possible to consider *Thompsonia* as a direct descendant of *Peltogaster socialis*, but the former genus may well have had an ancestor with many external sacs of normal Rhizocephalan type. A likely scheme of evolution is the following:

The typical Rhizocephalan with single external sac and single root system.

↓

Rhizocephalan with single root system but several external sacs of normal structure.

↓ ↓

Peltogaster socialis. Separate external sacs and root systems.	*Thompsonia.* A single root system and many externa sacs of simple structure.

In this remarkable life-history we find many phenomena which could hardly have been expected in so high a phylum as the Arthropoda. The analogy with the Fungi is strikingly shown in the mycelium-like root-system, producing its singular asexual reproductive organs, which are not dissimilar to the sporangia of a form like *Mucor*. A more convincing parallel may be drawn with a lower animal phylum, the Cœlenterata, where typical Hydromedusan forms, like *Obelia* and *Podocoryne*, produce medusa buds with a complex structure and germ cells differentiated *in situ*; while there are other genera, like *Eudendrium* and *Aglaophenia*, in which the medusoid individuals are entirely degenerate, with the simplest structure, and the germ cells are formed in the cœnosarc and migrate thence into the medusoids. If *Sacculina* and *Peltogaster* correspond roughly to the former class, *Thompsonia* occupies a place similar to that of the latter.

THOMPSONIA AND THYLACOPLETHUS.

When Coutière established his genus *Thylacoplethus* he remarked that in form it approaches *Thompsonia globosa* Kossmann:

> "Mais il doit en être séparé génériquement, même avant toute comparaison de la structure interne; *Thompsonia* a été trouvée fixée sur les pattes d'un Crabe (*Melia tesselata* Latr. provenant des Philippines), c'est-a-dire sur un Crustacé tres éloigné des Alphées dans la systématique, et d'autre part *Thylacoplethus* offre le premier exemple d'un Rhizocéphale aussi completement gregaire."

In spite of the very incomplete description of Kossmann's parasite, Häfele is almost certainly correct in identifying the Japanese form described by him as *Thompsonia*. There is only one serious discrepancy to be explained. In the type *T. globosa* only two external sacs were found upon the original host, while *T. japonica* is as "gregarious" as Coutière's *Thylacoplethus*. This is not a point, however, which weighs with me at all, for I know how easily these sacs are detached. There were probably a larger number present at the time of capture. The hosts were in both cases brachyurous Decapods and in both cases the parasites were attached to the thoracic legs. It seems, however, that *Thompsonia* is not like the other genera of Rhizocephala, the occurrence of which is confined in each case within a very narrow division of the Decapods, but enjoys a very wide diversity of hospitality; for Krüger reports that not only does *T. japonica* parasitise Brachyura, but is even found upon a hermit crab (*Pagurus striatus*). The two points, then, upon which Coutière lays such great stress are shown to be without importance by later work.

Why, then, did Häfele not recognise the identity of *Thompsonia* and *Thylacoplethus?* His negative decision rests upon points of difference in structure, but he makes some reservation owing to the unsatisfactory nature of Coutière's unillustrated account. I will quote his concluding sentence:

> "Gerade aber der Umstand, dass Coutière von einem 'Manteau à double paroi chitineux dans lequel est suspendue une masse viscérale, et qui porte une ouverture cloacale' spricht, lässt mich mit ziemlichen Sicherheit vermuten, dass in *Thylacoplethus* eine ganz andere Gattung vorliegt."

I am at a loss to understand why Häfele did not find an inner layer of chitin (the internal boundary of the mantle), but I think it will be found to exist in *T. globosa* when better preserved material is examined. With regard to the existence or non-existence of a cloacal aperture, this apparent difference is due to the fact that the organ appears only at a very late stage in development. But in any case I hardly think that, in view of the obvious agreement in structure and development, there could be any reason for separating generically *Thompsonia* (as described by Häfele) and the forms parasitic on Alpheids (as described by Coutière and myself). My own observations fail to reveal any difference between the parasites of Brachyura and Alpheids and an examination of the figures given by Häfele for *Thompsonia globosa* (for stages which the parasite of *Thalamita* does not show) and comparison with sections of corresponding stages in the Alpheid parasites show an essential similarity.

There is one point to which I refer further in the next section in Coutière's description of *Thylacoplethus*, but may be briefly mentioned here. It is the occurrence of parasites on the sternum and not on the appendages of the host. But this difference can hardly be conceived to be of generic value.

AMENDED DIAGNOSIS OF GENUS.

Thompsonia Kossmann (= *Thylacoplethus* Coutière).

A colonial Rhizocephalan infecting various Decapod Crustacea. Root system diffuse, widely distributed in body of host, sending branches into thoracic and abdominal appendages, which give off numerous sacs containing reproductive cells and becoming external at a moult of the host. These *external sacs* consist of a mantle and visceral mass without an intervening mantle cavity: mantle thin and devoid of muscle fibres. Visceral mass contains ovary only without generative ducts, testis, or nerve ganglion. Development probably parthenogenetic. Nauplius stage omitted from life-history, larvæ liberated at Cypris stage, after disintegration of the visceral mass, through apical cloacal aperture which appears in the mantle at a late stage. Moulting of host not prevented.

I will quote here the original description of Kossmann (6, Taf. v, Fig. II *a*):

"Die *Thompsonia globosa* entbehrt einer Mantelöffnung. Dagegen besitzt sie einen ausserordentlich langen Rüssell, welcher etwa in der Mitte seiner Länge einen Ring verdickter Cuticula zeigt. Der Körper des untersuchten Thieres war gänzlich reducirt, die Bruthöhle aber angefüllt mit Larven des Cypris stadiums, welche zwei Augen besassen. Die grösse des Thiers war sehr gering: 1.8 mm. Länge incl. des Rüssels zu 0.75 mm. Breite. Die beiden Exemplare nach welchen die obige lückenhafte Beschreibung gemacht ist, sassen beide, nicht am Abdomen, sondern an den Beinen einer *Melia tresselata*. Fundort, Aibukit, Palaos."

THE SPECIES OF THOMPSONIA.

The following is a list of the species which have been described up to the present:

	Host.	Place.	Lenth of external sac.
Thompsonia globosa Kossm.	Melia tessellata	Aibukit Pelews	1.8 mm.
Thompsonia (Thylacoplethus) edwardsi Cout.	Alpheus edwardsi	Thursday Island, Torres Straits.	
Thompsonia (Thylacoplethus) heurteli Cout.	Alpheus macrochirus	Fernando Veloso	4.5 mm.
Thompsonia (Thylacoplethus) sp.	Alpheus avarus	Torres Straits	1 mm. (young).
Thompsonia japonica Häfele	Pilumnus sp	Japan	2 mm. elongated.
	Pagurus striatus	Japan.	
Thompsonia affinis Krüger	Diptychus sp	Japan	1 mm. round.

This list does not include the parasite mentioned by Spence Bate as occurring on *Alpheus digitatus* from Fiji. It appears to be a species of *Thompsonia.*

I next give a tabular statement of the forms of *Thompsonia* which I have seen myself and the characters in which they differ:

Species on which the forms occur.	Localities.	Differences in characteristics.
Synalpheus brucei	Murray Island, Torres Straits	External sac, pear-shaped, pink, 1 mm. long. Cypris.
Actæa ruppellii	South Africa	External sac, pear-shaped to round, 1 mm. long.
Thalamita prymna	Murray Island, Torres Straits	External sac, elongate, lemon-yellow, 3 mm. long. Cypris.

It is, I think, very difficult to establish specific distinctions until more material of *Thompsonia* has been collected and compared. At present one can not say how far the character of the host affects such superficial characters as size, shape, and colour. I think that in the three forms which I have examined we very possibly have three distinct species, but I refrain from burdening systematic zoology with fresh names when we know so little about the validity of those already given.

One point in Coutière's description of *Thylacoplethus* may have an important bearing on the systematic question. In the three Alpheids which he examined the parasites were, he says, situated on "les quatres premiers pléosternites, qui se montrent soulevés en un large bourrelet transversal." And he contrasts this with the form, certainly very near and probably identical,* which Spence Bate mentions and figures in the *Challenger* monograph on the Decapoda, occurring to the number of 30 individuals at the base of the abdominal appendages of *Alpheus malleodigitatus* from Fiji. The parasites which I describe from *Synalpheus* are also confined to the appendages and are therefore, if I read Coutière's account aright, much more like the *Challenger* form than are those of the French investigator. It is possible that a section of the genus is characterised by the occurrence of the external sacs on the sternum rather than on the appendages.

THE INFLUENCE OF THE PARASITE ON THE HOST.

So far as my material goes, the effect of the parasite upon the host is negligible. The gonad does not diminish in size and in some cases at least does not cease to function. One female Alpheid which I collected had both fertilised eggs and parasites upon her abdominal appendages. This was probably an exceptional case.

The secondary sexual characters do not undergo any change. The specimen of *Thalamita prymna* was a heavily parasitised male, but the abdomen showed no broadening, assumption of female appendages, or diminution of copulatory appendages. In the Alpheid *Synalpheus brucei* the abdominal appendages do not differ in the two sexes and the female is to be distinguished from the male only by the greater width of the abdomen and better development of the pleura. This character is not affected by the parasite.

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*Spence Bate did not think that his parasite was related to *Sacculina* because the embryo exhibited no Crustacean affinities. Development must have been at a very early stage; the general appearance and position are so unmistakably those of *Thompsonia*.

SUMMARY.

(1) The root system of *Thompsonia* is continuous throughout the body of the host, whatever the number or stage of development of the external sacs may be.

(2) Where they penetrate the appendages the roots contain fewer yolk globules and the lacunar space is filled with germ cells. Besides the external sacs, there are a number of terminal swellings in the tissue of the appendages. These are similar in structure to the external sacs and become external at a subsequent moult of the host.

(3) The external sacs consist of a mantle with an external and internal cuticular investment and a visceral mass mainly occupied by the ovary. No mantle cavity is found between the mantle and visceral mass.

(4) There is no testis, development being in all probability parthenogenetic. The egg is lightly yolked and gastrulation takes place by epibole. The Nauplius stage is omitted from the life history, the young hatching at the Cypris stage.

(5) During development the visceral mass disintegrates so that at the time of hatching the mantle contains a great number of Cypris larvæ ready to emerge. An apical perforation is made in the mantle, and on the moult of the cuticle a way is thus opened to the exterior for the larvæ.

(6) The escape of the larvæ is contemporaneous with or soon followed by a moult of the host. The empty shells of external sacs are carried away with the cast skin, and the terminal swellings of the root system emerge as a new crop of external sacs.

(7) Development of the germ cells in the lacunar tissue of the roots may take place *in situ* as well as in the external sacs, but it does not apparently proceed very far.

(8) The large number of external sacs in both *Thompsonia* and *Peltogaster socialis* is accounted for by a process of internal budding from a single original larva.

(9) *Thompsonia* is not a primitive Rhizocephalan, but a very specialised form.

(10) The genus *Thylacoplethus* Coutière is synonymous with *Thompsonia* Kossmann.

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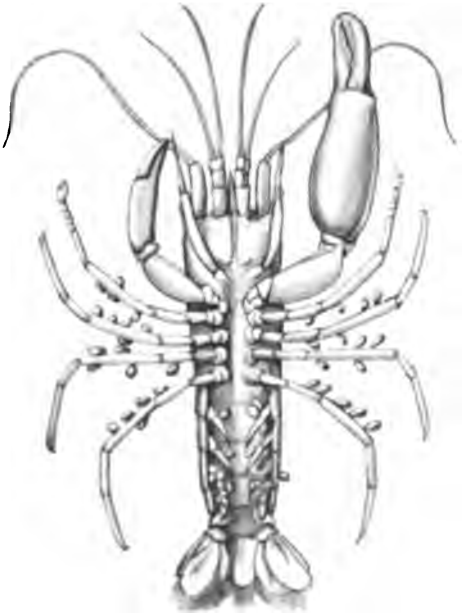

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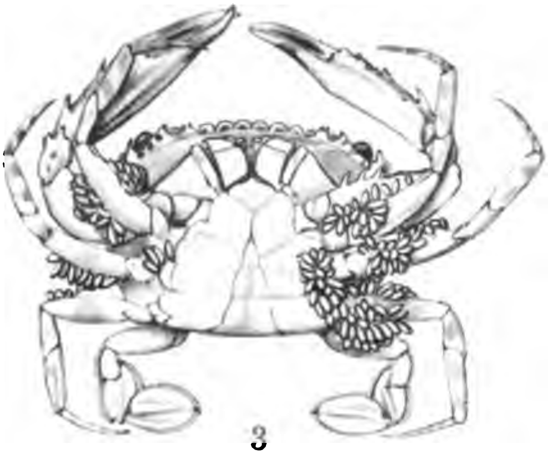

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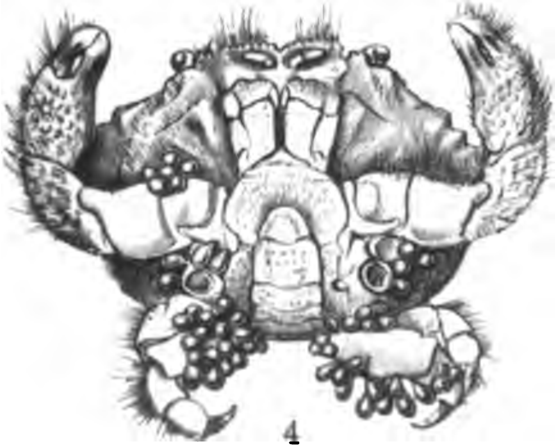

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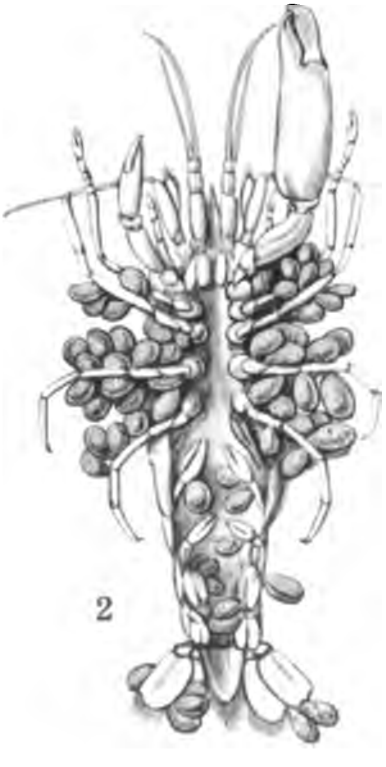

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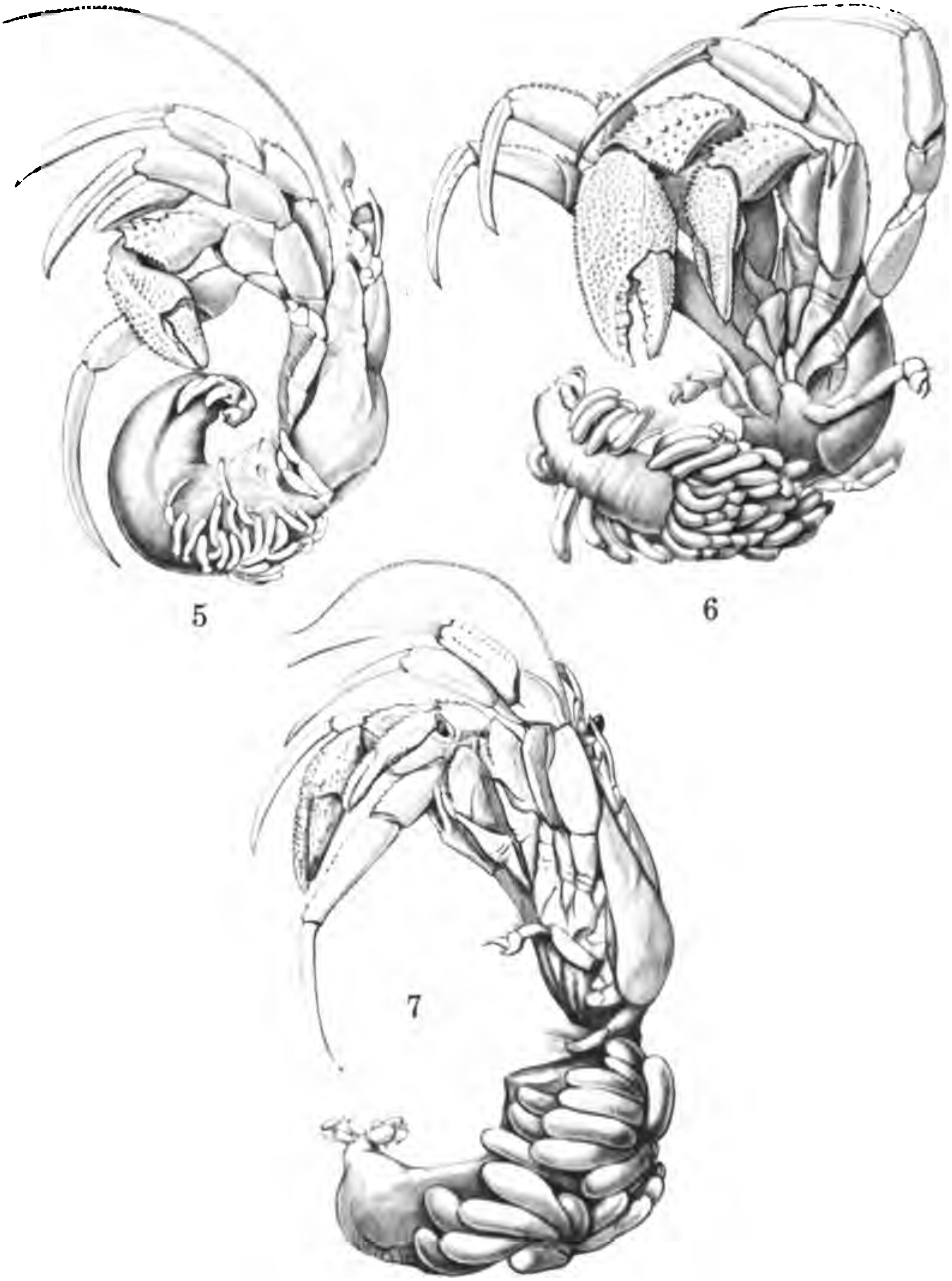
Fig. 1. Thompsonia on Synalpheus brucei. Young external sacs on the abdominal and thoracic appendages. x 3.

Fig. 2. The same at a later stage. The external sacs now contain Cypris larvæ which are roughly indicated within. x 3.

Fig. 3. Thompsonia on Thalamita prymna. To show the very large number of external sacs occurring on this specimen. Natural size.

Fig. 4. Thompsonia on Actæa ruppellii. External sacs pear-shaped. x 2.

The first three specimens figured are from Murray Island, the fourth from South Africa.



Peltogasterella socialis, Krüger.

Figs. 5, 6, and 7. Stages in growth of the external sacs of Peltogasterella socialis, on Pagurus alaskensis. x 2. Friday Harbour, San Juan Archipelago, State of Washington, U. S. A.

II.

HAPALOCARCINUS, THE GALL-FORMING CRAB, WITH SOME NOTES ON THE RELATED GENUS CRYPTOCHIRUS.

BY F. A. POTTS, M. A.
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Three plates and nineteen text-figures.

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HAPALOCARCINUS, THE GALL-FORMING CRAB, WITH SOME NOTES ON THE RELATED GENUS CRYPTOCHIRUS.

By F. A. Potts, M. A.

HAPALOCARCINUS MARSUPIALIS Stimpson.

INTRODUCTION.*

Hapalocarcinus is a genus of Brachyrhynch crabs, the individuals of which are very small in size and profoundly modified, owing to the fact that they pass the greater part of their lives confined in small cavities in coral colonies. At an early age the female crab settles between two adjacent branches, usually terminal, and so influences their further growth that they broaden and, later, unite to form the so-called gall, a lenticular or spherical structure about the size of a hazel nut. Within this is the living chamber of the crab, which communicates with the outside water by a series of apertures. The animal thus becomes sedentary, never leaving its gall and producing enormous broods of larvæ.

Hapalocarcinus marsupialis was first described by Stimpson between 1856 and 1859 from specimens "found clinging to the branches of living madrepores in the harbour of Hilo, Hawaii." It was thus thought at first to be a free-living animal, but Verrill, in 1867 (6), pointed out that certain "deformities on corals," compared by Ehrenberg to the galls formed by the influence of insects on plants, are in fact caused by Stimpson's *Hapalocarcinus*. He describes the phenomenon in the following passage:

> "Another peculiar mode of parasitism I have observed in a singular crustacean (*Hapalocarcinus marsupialis*, Stimpson) from the Sandwich Islands. This creature lodges itself among the slender branches of a coral (*Pocillopora cæspitosa*, Dana) and causes, probably by its incessant motions, the branches to grow up and often interlock above, leaving openings between them suitable for the uses of the parasite but usually too small to allow of egress. Most specimens of the corals of this species sustain one or more and often numerous examples of these curious enlarged bulbs among the branches."

In subsequent papers (7, 8) he makes further observations on the occurrence of "galls," without adding much to the above description.

Karl Semper became well acquainted with *Hapalocarcinus* (and the related form *Cryptochirus*) during his researches in the East Indies. In his well-known book on "The Natural Conditions of Existence as they Affect Animal Life" (published in English, 1881) he illustrates the influence of constant currents on the growth of coral by the formation of galls and the modification in the shore of coral reefs. In the former case the current is produced by the respiratory movements of the crab. The recognition of the definite factor in gall production is thus due to this author. A description (and, in some cases, figures) of the galls formed in *Seriatopora*, *Sideropora*, and *Pocillopora* is given, but it is somewhat incomplete and not always correct in details. But the great merit of having pointed out the interest of the form belongs to Semper.

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*His duties as an officer in the English Army made it impossible for Mr. Potts to correct the proof of this paper.—A. G. M.

Passing over one or two short notices of the genus, we come to a paper by Calman (2) which gives a thorough description of the external features of the adult female, from two or three individuals collected by A. C. Haddon in Torres Straits. An important part of this contribution relates to the systematic position of the genus. In various points, particularly the structure of the third maxilliped, *Hapalocarcinus* occupies a very isolated position among the Brachyura Brachyrhyncha. These peculiarities it shares with *Cryptochirus*, another coral-inhabiting crab, which is discussed in the second part of this paper. The two genera are therefore united to form the family Hapalocarcinidæ. The galls examined by Calman were situated upon a species of *Seriatopora*; they are figured and described, but as preserved material alone was inspected not much of importance with regard to the biology could be added to Semper's account. The series of individuals was too small for all points of structure to be examined. About the reproduction of the form Calman says:

> "The fact that each gall is inhabited by a solitary female, while the male is as yet unknown, would seem to indicate that the sexes are at first free-living and that it is only after impregnation that the female becomes imprisoned in a gall. The fact that the youngest gall observed is of ample size to contain a full-grown *Hapalocarcinus* tends to confirm this suggestion."

In the spring of 1913, when I was preparing to join the Carnegie Institution Expedition to Torres Straits, Dr. Calman was kind enough to point out to me the interest attaching to the natural history and reproduction of the Hapalocarcinidæ. During our stay at Murray Island, from September 22 to October 27 of that year, I was able to obtain an abundance of material and make some new observations on the biology.

Hapalocarcinus lives in great numbers on the reefs of Murray Island at the north end of the Great Barrier Reef of Australia. It here forms galls on at least two species of branching Madreporarian corals, *Pocillopora cæspitosa* and *Seriatopora hystrix*, both belonging to the same family, the Pocilloporidæ, and characterised by dichotomous branching. Both are widely distributed and dominant forms, but the former, a beautiful rose-coloured coral in life, is the favourite host of the gall-forming crab. In the still waters of the inner reef there is hardly a colony which does not bear at least one of the galls, while some show nine or ten in various stages of development. The ease with which the growth of the colonies can be modified by external agencies accounts for the attraction which *Pocillopora* possesses for *Hapalocarcinus*. No coral shows more variation under different environmental conditions. If colonies of *P. cæspitosa* from the outer edge of the reef are compared with those which grow in the sheltered inner waters it is difficult to believe that the two forms can be embraced within a single species. The compact colonies with short thick branches in the former situation owe their form to the strong wave action, while the long and slender branches which the coral develops when out of reach of the breakers are correlated with the absence of strong currents within the reef.

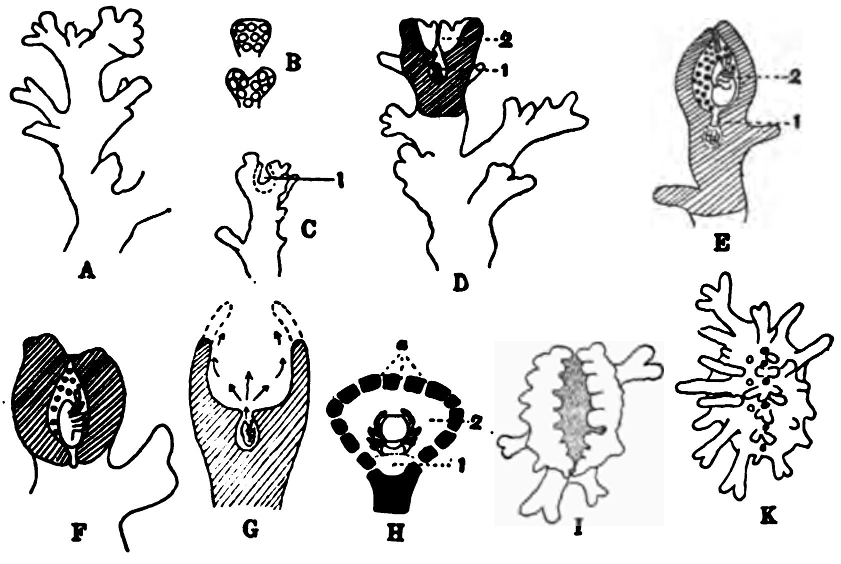

Fig. 1.—Various stages of gall-formation in *Pocillopora cæspitosa*.

A. Normal branch of colony.
B. Tip of growing branch in two stages, showing dichotomous division.
C–F. Galls in side view to show both the component branches.
C. First stage of formation of a gall; the dotted line indicates the extent of the chamber 1.
D. A typical "open" gall: chamber 1 inhabited by crab, chamber 2 in course of formation. In this and the following figures E–G the gall has been cut in vertical transverse section and ground down by stone. The shading shows the ground surface.
E. A "closed" gall with chamber 2 completed and occupied by the crab; chamber 1 deserted and partially filled up by spongy cœnenchyme. The black spots show the position of the thecæ of the coral.
F. An older "closed" gall showing increased thickness of walls and restriction of interior space.
G. Diagram of an "open" gall to show the way in which the respiratory current influences the growth of the coral. The arrows represent the expired current, the dotted lines the direction the growth of the walls will take.
H. Diagram of "closed" gall in plane of union of the component branches, showing the relation of the inhabitant to the apertures, *a*, *a*, *a*. A complete series like this is found in the earlier stages of closed gall, but becomes interrupted later.
I. View of an "open" gall from above, showing the converging laminar branches; their border is seen to consist of a series of short processes. One or two twigs have been formed on the outer surface.
K. View of "closed" gall from above, showing apertures as black spots and twigs arising from all over the outer surface of the gall.
All the above drawings are natural size except of B and G, which are slightly enlarged.

Seriatopora, on the other hand, shows less power of response to external conditions. While it flourishes most luxuriously on the mid regions of the great reef flat at Murray Island, it rarely approaches within a hundred yards of the edge, as does *Pocillopora*. Galls are by no means so common on its colonies, for they represent a much greater interference with the normal type of branching. The introductory remarks, then, which follow are confined to *Pocillopora*, the abundance of the material of which gave exceptional facility for study.

In the first place it may be stated that the galls themselves vary greatly in development and that there is a general correspondence between the stage of development and the size of the crab it contains. In all cases the gall appears to be formed and inhabited by a solitary female individual. Those in the younger "open" galls, where the two constituent branches have not yet approached each other and fused, are immature; those in the older "closed" galls are mature, and often the abdominal appendages are laden with developing eggs.

THE GALLS IN POCILLOPORA CÆSPITOSA.

The young female crab probably commences its sedentary life by settling down in the notch at the apex of a recently divided branchlet. She is at this period a small flat creature, little more than a millimetre in carapace length. Her position at the growing point allows her to control the future development of the branch. To estimate the extent of her influence a more exact description of the *Pocillopora* colony must be given. Though the method of branching is certainly dichotomous, it is very irregular. If we first of all take the still-water type of colony, here the main branches are comparatively slender, not more than 5 to 7 mm. in diameter. Dichotomy is well shown in some of the main divisions. It is always exhibited in the growth of the lateral and terminal twigs, which closely beset the main branches. These twigs are usually 3 to 4 millimetres long and not more than half a millimetre in diameter. In the course of their growth they are at first quite cylindrical; then they become palmate, and finally, as growth is checked in the middle, division takes place and two short equal divisions are formed. The space between these when they assume their palmate shape is sufficiently large to accommodate and partially protect so small a creature as the young *Hapalocarcinus*.

When the colony lives in troubled waters its form changes considerably. The main branches are much shorter and stouter; the twigs which cover their surface are more numerous and more closely set. They do not exhibit dichotomy, but always remain cylindrical and do not broaden out apically, so that they do not promise good shelter to a householder whose size increases so rapidly as does that of *Hapalocarcinus*.

When the crab settles down the effect of its presence is very soon felt. The two branches, instead of diverging at an angle, remain at an equal distance apart. The initial tendency of the branch to broaden out is encouraged, but at the same time the tendency to dichotomous branching is suppressed. There are thus formed two broad expansions, which approximate above and laterally, thus partially enclosing a chamber large enough to contain the crab with comfort. In the diagrams which illustrate this paper this chamber is referred to as *A*.

In the second stage of construction of the gall a much larger upper chamber (*B*) is formed by the continued growth of the two branches. During nearly the whole of this time, however, the crab remains an inhabitant of *A*. It is not until the two walls of the upper chamber have almost met that she finds her earlier quarters too restricted and transfers herself to the upper chamber at the time when it is ready for occupation. Just before fertilisation, which occurs shortly after this removal, the ovary begins to grow rapidly, causing so great a development of the abdomen that more spacious accommodation is quickly needed and provided for in the new chamber.

It is rather difficult to explain the precise influences which give the gall its characteristic and constant shape, but it can be stated with certainty that if the respiratory current of the crab is not the sole external factor which is responsible, it is at least the most important. The initial modification of growth may be due in part to the mere mechanical effect of the continued presence of the crab, but I think even here the respiratory current is more effective. By means of powdered carmine spilt in a small quantity of sea-water containing a crab I was able to convince myself that, as a general rule, the water needed for respiration is sucked into the branchial chamber behind and expired upwards and outwards, as usually happens in the Brachyura. Even at the very first, we must suppose that the crab never forsakes its position in the saddle between the two branchlets. It may move laterally, but always in the same plane. Later, when the initial cavity *A* has taken shape as a narrow crevice, movement except in the one plane becomes an impossibility. Thus the original expiratory current always flowing upwards and outwards has sufficient fixity of direction and constancy of power to secure a definite result.

In the first place, then, the effect of a vertical current of water flowing between the two branchlets is that the further growth of these tends to follow the borders of the stream, so that they approximate and do not diverge. With regard, however, to the formation of the larger chamber *B*, the crab enters into occupation only at the completion of the work. It follows, then, that here she must influence the growth of the branches in a more indirect, though quite effective manner. The expiratory current either flows straight upward through the entrance to chamber *A* or impinges on the lip. In the first case its velocity would be checked and it would tend to disperse on entering the larger body of water. Or if it strikes the lip of the chamber it would be deflected obliquely toward the opposite side. In either case the effect will be to secure a diverging current issuing from the aperture which will repress growth on the inner edge of the branch though not on the outer. As the outer edges become built up the divergent currents will become circular eddies and the growth of the wall of chamber *B* will follow their outside line. The two opposed walls meet naturally at the intersection of their curves, but that part of the current which flows directly upwards prevents their entire concrescence. But after the crab has migrated into chamber *B*, partial fusion does occur, so that what was at first a wide slit is converted into a series of small circular holes occurring laterally as well as above, and all of equal size and, presumably, importance. This partial closure of the slit is brought about by the fusion of the small processes on each side with those of the other. These processes are as a matter of fact the twigs springing from the modified branches. The effect of the current is not to prevent branching but to increase laterally the growth of the branch. The border of the branch is always lobate, each lobe indicating a twig which is not allowed to individualise, owing to the continued growth of the branch. On the outer side of the gall well-formed twigs are common. In fact, one may say that in the formation of galls the branching is masked by the immediate union of the secondary branches to form a continuous wall.

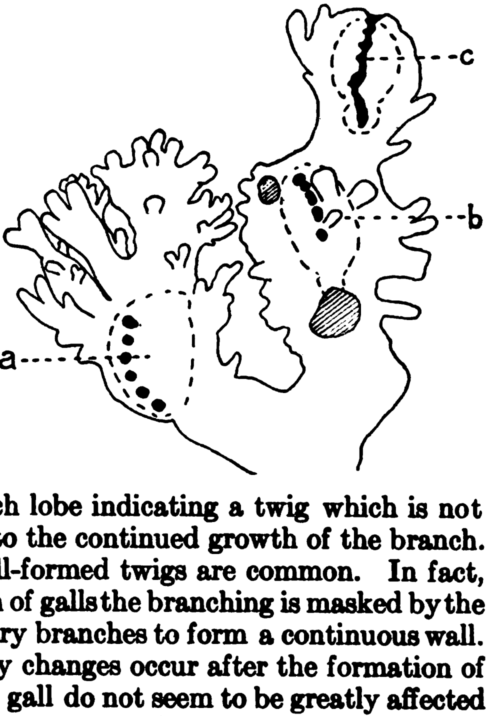

FIG. 2.—Old established galls in a colony of *Pocillopora cæspitosa*.

The black spots (or line) represent the respiratory apertures (or fissure), the dotted circles within the shape of the cavity of the gall. *a* and *b* are old galls, as is shown by the well-established systems of branches which spring from their surface. In the case of *b* one of the daughter branches, which must have started to grow after the formation of *b*, has itself been modified to form a gall, which is nearly closed. Very possibly, then, *b* and *c* represent successive generations of *Hapalocarcinus* and afford some indication of the ratio of growth as between the coral colony and its commensal. ×¾.

A certain number of secondary changes occur after the formation of the gall. The polyps inside the gall do not seem to be greatly affected by their life within a closed dark space (fig. 4) and the thickness of the cœnenchyme is added to very distinctly on the inside as well as the outside, so much so as to encroach seriously upon the space in chamber *B* and partially fill up the disused chamber *A*. This secondary growth restricts and eventually stops the lateral movement of the female crab, which at that time will have obtained an enormous bulk. The formation of the gall does not put an end to the further development of the branch of which it forms part. A perfect forest of twigs covers the surface of galls of some standing and occasionally examples are to be observed in which the gall is the foundation of a complex branching system. In these cases the galls can evidently lay claim to a respectable antiquity. As long as the crab lives the cavity remains in connection with the exterior by means of the circle of apertures. Sometimes a gall is seen where the crab is dead and all apertures have closed up.

THE GALLS IN SERIATOPORA HYSTRIX.

This coral grows only in the sheltered waters of the inner reef, though very widely distributed there, and there is little modification of the manner of branching. The colony consists of slender cylindrical branches of approximately equal diameter, diminishing slowly towards the sharp apex. It has then a very spiky appearance. The branching is regularly dichotomous and where adjacent branches come into contact they fuse, as is seen in the accompanying figures. Where branching takes place at the apex the space between the branchlets is entirely inadequate to shelter even so small a creature as the young *Hapalocarcinus*. For this reason the galls are found not at the surface of the colony, as in *Pocillopora*, but between more basally situated branches where a broader lodgement is offered.

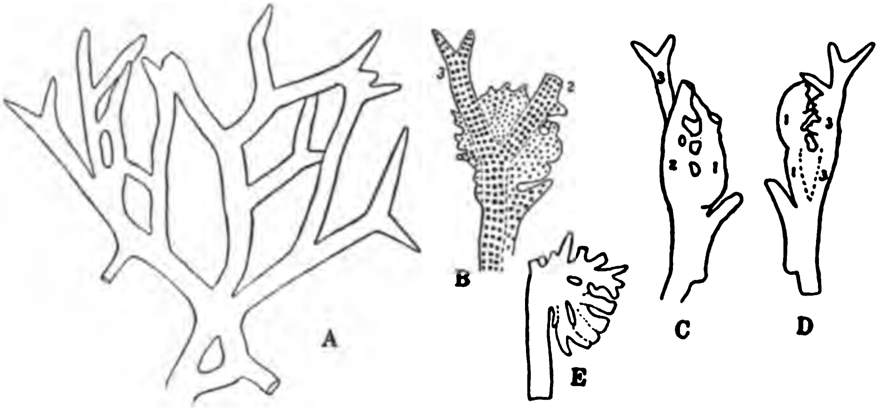

FIG. 3.—Gall-formation in *Seriatopora hystrix*.

A. Fragment of normal colony, showing dichotomous branching and fusion of adjacent branches.
B, C, D. Views of a single gall formed at the junction of three branches, 1, 2, 3.
B. One of its component laminæ formed by growths of cœnenchyme from branches 2, 3; the outlines of these branches are still preserved; the black spots show the thecæ of the colony regularly arranged on the original branches; not so much so on the new growths.
C. Side view showing processes from branches 1, 2 fusing together.
D. Similar view of other side, showing junction of processes from branches 2, 3.
E. Another gall, showing how each lamina is made up of a number of small branches fused together. (From a specimen in the Cambridge University Museum of Zoology.) Natural size.

When the crab is established a very marked interference with the growth of the coral takes place. The normal growth is greatly stimulated, a much more considerable addition to the cœnenchyme appearing than would be made in the normal thickening of the branches. Thin laminar expansions grow out from the sides of the branches in a plane parallel to that of the crab's respiratory current. These laminæ do not, however, represent continuous growth, but are formed by the coalescence of parallel twigs which can be easily distinguished at the edge of lamina. This is perhaps best illustrated by a specimen in the Cambridge University Museum of Zoology, which is shown in figure 3E. The numerous gaps which occur in the walls of the gall are due to the incomplete fusion of the component twigs.

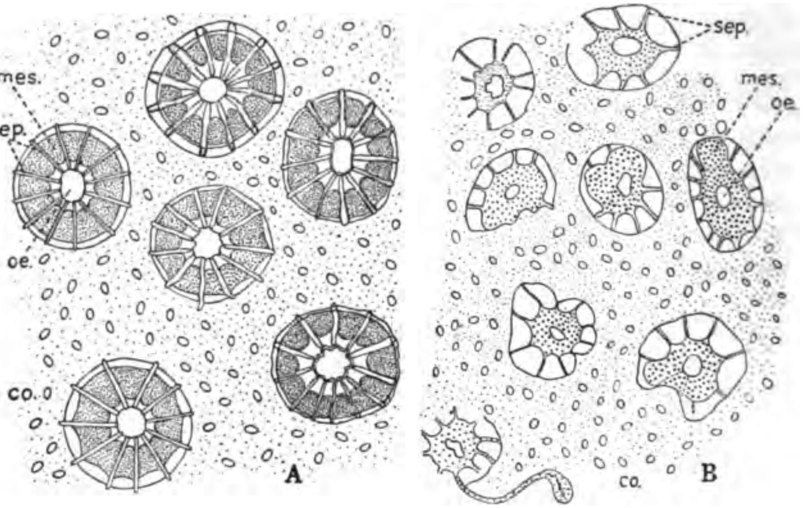

FIG. 4.—Surface view of colony of *Pocillopora cæspitosa*.

A outside and B inside a gall. ×20. After prolonged decalcification, preparations stained with borax-carmine.

In A the polyps are regularly developed, the tentacles and mesenteries are formed of thick, deeply staining tissue and the septa are of normal number and symmetrically arranged.

In B the polyps are stunted and irregular, the mesenteries and tentacles not well developed and the septa often placed asymmetrically and sometimes short of the typical number. *co.*, cœnenchyme,; *oe.*, œsophagus; *mes.*, darkly staining tissue, mesenteries and tentacles indistinguishable; *sep.*, septa.

The initial result of the interaction of the crab and the coral is the production of a small initial chamber as in *Pocillopora*. Afterwards an upper chamber is formed, large enough to contain the mature female. The complete gall is not quite so regular as that in *Pocillopora*, but it has essentially the same structure.

At first sight the interference with the normal habit of branching involved in gall formation seems to be much greater in *Seriatopora* than in *Pocillopora*. In the latter case there is an apparent broadening of existing branches, a stimulation of lateral growth as compared with apical growth. In the former, however, there is at the point of settlement a production of numbers of tiny lateral branches which, together with the main branches from which they spring, form the walls of the gall—a basketwork the meshes of which are filled in by subsequent growth. The course of the main branches can always be traced, even in the fully formed gall. But as I have indicated above, in *Pocillopora*, too, there is really an increased branching masked by immediate fusion of the branches, so that the process of gall formation is not essentially different in the two genera.

It is rather difficult to follow the account of gall formation in *Seriatopora* given by Semper in "Animal Life." This book represents a course of lectures given at the Lowell Institute in Boston in 1877 and I am not able to say whether a German edition of the book was ever published. The English work has, however, suffered very badly at the hands of the translator and it is sometimes difficult to determine what Semper intended to say. Take for instance the following sentence: "A diseased excrescence is first produced by the crab establishing itself between two branches, and the twig thus originating takes various forms according to the character of the species of coral." What seems to be meant is that when the young crab establishes itself between two branches it modifies and stimulates the growth of each of them and the modified branches (twigs) take on various forms according to the species of coral which is in question. This is of course perfectly true and corresponds to what I have said in the preceding accounts. The idea that the growth brought about by *Hapalocarcinus* is pathological is given in the application of the ungraceful term of "diseased excrescences" to it. This is entirely unwarranted, since similar modifications affecting the whole colony take place under the influence of wave action. There is, moreover, no reason for calling the crab a parasite, since it does not live upon the tissues of the coral; but even Calman falls into this error.

Semper, after describing the process by which an open is converted into a closed gall, makes the following remarks:

> "The creature requires a constant and rapid renewal of the water in the gall in which it lives, for the purpose of respiration; at first the water finds a free passage on all sides, but when the two twigs have bent over towards each other, the space through which it can find entrance and exit must grow narrower and narrower. Moreover, from the structure exhibited by galls broken off from the coral, it may be concluded with certainty that the crab moves about very little in the cavity, for otherwise we should not find the very distinct scars which are evidently produced by continual scratching in one spot. Since, in all the crabs of this group, the current of water for breathing enters the body close to the mouth, and passes out again at the hinder margin of the branchial cavity, the stream passing through the gall must always flow in one and the same direction. The results are easily recognisable in the half or wholly closed gall. The two excrescences on the coral grow together quickest in those spots which are least exposed to the current through the gall; there also they first come into contact, till at length only two fissures, more or less wide, are left, which plainly show, by their position opposite to each other, that it is through them that the current for respiration passes; one fissure serves for the influx, the other for the exit, of the water. These two slits remain open so long as the crab is alive; no living crab is ever found in a closed gall, and they are for the most part perfectly empty."

The main criticism of the above statement which I should like to make is that Semper is mistaken in supposing that the crab moves about so little in the cavity that one or two small fissures or apertures alone suffice for the respiratory current. In my experience, in *Pocillopora* the cavity is large enough for the crab to move about a good deal in one plane and by observing the inhabitant of a nearly closed gall I could actually follow such movements. I have never seen such scars as Semper describes as due to the "continual scratching in one spot," nor did Calman. In saying that "as in all the crabs of this group" (whichever group is meant) the respiratory current enters the branchial cavity anteriorly (close to the mouth) and passes out posteriorly, the case is exactly the reverse. Why it should be stated that both the exhalant and inhalant streams should always flow in one and the same direction I can not understand. As stated above, experiments with carmine particles show that the exhalant current flows upwards and outwards and the inhalant current laterally. Finally, in no galls that I have seen are the apertures reduced to two. In *Pocillopora* there is nearly always a considerable number (up to 10), of equal size and presumably importance, situated along a line which encircles the gall but which is interrupted by the stalk. Only in a few old galls where internal growth has restricted the space do some of the apertures close up.

GALL FORMATION IN STYLOPHORA AND SIDEROPORA.

A species of *Stylophora* (*S. raristella* Dep. var *wilsoni* J. S. Gard.) in the Cambridge Museum shows very well the formation of galls in branching corals where the branches are more massive than in *Pocillopora* and *Seriatopora*. The gall is produced apically, the branches broadening out as in *Pocillopora;* but when fully formed the gall is hardly distinct from the branch which bears it, its breadth and width being little greater. The completed gall differs, moreover, from that of *Pocillopora* in the fact that the approximated lips never show local fusion, a narrow fissure of uniform width remaining between them throughout the life of the gall crab. Here, then, the gall is truly formed by the broadening of existing branches and not by the production and fusion of new ones, and this is due to the larger scale of branching characteristic of the genus. This description applies also to the genus *Sideropora,* as far as can be seen from the account and figures given by Semper of galls in *Sideropora palmata* (p. 218, fig. 67); they also occur in *S. digitata.*

ACTION OF RESPIRATORY CURRENT ON INDIVIDUAL POLYPS.

Speaking of the thecæ which occur in the interior of the walls of the gall, Semper says:

> "Not one of the cups is normal in structure; the depression, which in the external polyps is very deep, is here no more than a shallow pit, and the *septa* (or party walls) of the cup are very slightly developed. Hence it follows,

with some degree of certainty, that the polyps on the inner surface were not able wholly to overcome the resistance of the current passing over them. This direct action of the stream is unmistakable in many of the cups, where the polyps were exposed to the greatest force of the current produced by the crab; for they are placed obliquely on the fissure and directed outwards, as they must have grown, supposing them unable to grow against the stream."

The current, then, Semper thinks, modifies the direction of growth of the polyps.

Calman says that in the galls examined by him, the thecæ of the inner surface are, "as Semper states, small and shallow and have the septa only feebly developed. They are also in some parts distorted and drawn out to an elliptical outline, but this distortion does not appear to be definitely related to the marginal aperture of the gall as described by Semper, who attributes it to the action of the current of water caused by the crab." This qualifies the force of Semper's conclusion. In *Pocillopora* there is certainly a remarkable difference between the polyps on the inside and outside of the galls (fig. 4). This is seen on examination of both the hard skeleton and the soft parts. Semper's and Calman's observations were made on the former; and my own agree with them. Inside the gall the thecæ are shallower, sometimes prolonged towards the border of the gall, and differ considerably in size. The septa are less distinct. There is a larger amount of cœnenchyme intervening between the thecæ. A considerable disturbance of the normal method of growth, due to the respiratory current of the crab, is clearly shown.

The soft parts of the colony were studied after decalcification in 70 per cent alcohol with a small amount of nitric acid. Total preparations of the superficial tissue were made, staining in borax-carmine and mounting in Canada balsam. On the outside of the gall the polyps are regular in shape and position; they are nearly all of the same size. Internally a large proportion are small, though they usually have the total normal number of mesenteries and can not be regarded as juvenile. The larger polyps have not the regular shape characteristic of the normal forms. The examination of these preparations shows that the main effect of the current is direct repression of growth. The polyps which are formed are not allowed to attain the normal size. The distortion which they undergo is quite a secondary and unimportant effect.

Certain points of structure will now be described which shed some light on the biology of *Hapalocarcinus*. The first is the curious nature of the buccal area and the appendages surrounding it. Stimpson in the original description mentioned the large buccal area occupying nearly the whole breadth of the carapace and the third maxillipeds "with the ischium large and dilated within, while the merus is very small and slender like the three last joints."

Calman says:

> "The buccal area is very large, extending across the whole width of the carapace in front. Its anterior margin is sinuous, curving forwards on either side below the eye and taking the place usually occupied by the inferior margin of the orbit. The median part of the buccal margin approaches so closely to the base of the antennules that an epistome can hardly be said to exist. The third maxillipeds do not nearly cover the buccal cavity, and are widely separated from each other at the base by a semicircular area of the sternum. The ischium is flattened, subtriangular in shape, widening gradually from a narrow base, and having its antero-internal angle produced forwards, rounded, and fringed with setæ. The merus is articulated at the outer end of the distal margin of the ischium, and is less than half the width of the latter, hardly wider than the succeeding joints, and but little flattened. The exopod is rudimentary, being a simple lobe about half the length of the ischium. The epipod is well-developed. The second maxillipeds have the basal part of the exopod much expanded. In the first maxillipeds, also, the same part is very stout and much stronger than is usual in this appendage, while the inner lobe or endopod is small and subtriangular."

But no mention is made here or elsewhere of the maxillæ and mandibles. Calman had so little material that he was unable to investigate this point. But in the related genus *Cryptochirus* Heller had discovered and figured these appendages so long ago as 1861. They are of a very remarkable type, and as this is practically identical in the two genera I quote the passage in which he describes them:

> "Die beiden Maxillen sind ebenfalls blättchenförmig, ebenso die nach innen stark verbreiterten und mit geradem scharfen Kaurande versehenen Mandibel. Der Stiel der letzteren bildet mit der kauplatte einen starken Winkel, ein Palp fehlt."

When I came to examine *Hapalocarcinus*, not knowing the above passage, I was at once struck by the fact that each member of the two pairs of maxillæ is reduced to a single elongated plate while the mandible is without a palp and has not the robust biting character of the usual Decapod mandible.

Before describing these organs in detail I will state what, in my opinion, is the reason for their anomalous condition. So striking is their divergence from the very uniform Brachyuran type that a definite explanation is to be expected. This is without doubt to be found in a change in the feeding habits of the animal during its recent evolution caused by its voluntary imprisonment in an almost totally closed space. The usual diet of crabs, the comparatively large fragments of animal or vegetable substance, is denied to *Hapalocarcinus*. There is no doubt, indeed, that this form must live on the plankton which is drawn into the gall with the respiratory current, and since in the "closed" gall the holes which allow entrance to the interior are exceedingly small in the skeleton and must be smaller still if we allow for the coating of living cœnosarc, it is evident that the larger constituents of the plankton will be unable to pass through them. *Hapalocarcinus* is thus an example of the class of microphagous organisms and shows the kind of modifications which occur in them. In the account which follows I have compared those structures, where difference is exhibited, with the typical forms in the Brachyura.

THE GENERAL CONFIGURATION OF THE BUCCAL AREA.

In the Decapoda Brachyura the third maxilliped is so enlarged as to cover the whole of the buccal area. In *Cancer*, for instance, the two appendages form a pair of folding doors meeting exactly in the middle line and when they are closed the mouth and all the buccal appendages are completely hidden from view. In the endopodite the ischiopodite and meropodite are much broader than the more distal joints and together with the basal joint of the exopodite they form the greater part of a rectangle so perfect that the inner borders can meet exactly and the outer make straight hinge lines. This well-fitting apparatus ensures that the food, where this is taken in large pieces, can be masticated without the particles escaping. In some Brachyura, members of the Oxyrhyncha (e. g., *Stenorhynchus* and *Inachus*), where, owing to the shape of the cephalothorax, the buccal area is greatly diminished in width, there is not this excessive broadening of the two basal joints of the endopodite. In *Stenorhynchus* the meropodite is no wider than the succeeding joints, while the ischiopodite is but slightly broadened and has a curved inner border. But the three distal joints bend downwards

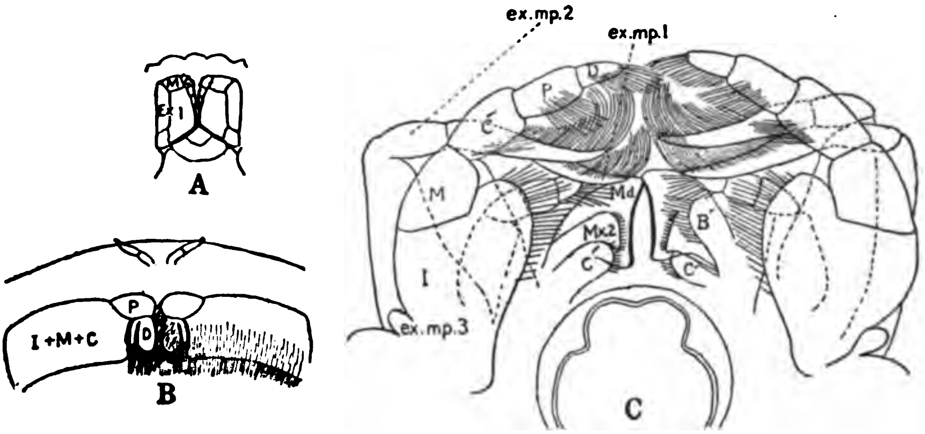

FIG. 5.—Various types of buccal areas in the Brachyura.

A. *Cancer*, ×1. B. *Pinnotheres*, ×3.5. C. *Hapalocarcinus*, ×85.
ex. mp. 1. ex. mp. 2. ex. mp. 3. exopodites of maxillipeds 1, 2, and 3;
B', *C'*, basipodite and coxopodite of maxilliped 1; *Mx2*, maxilla 2; *Md.*, mandible. Other letters as in text-fig. 16.

In A and B the other appendages are completely covered by the third maxilliped, and so they are not indicated in any way. In C, which is drawn from a specimen cleared in potash and mounted in Canada balsam, a great number of the buccal appendages are clearly visible and the character of the preparation allowed me to indicate by dotted lines the parts which were overlapped.

and help to rectify the inner border and internally the appendage is thickly provided with short hairs, so that though the appendages do not meet exactly in the middle the effectiveness of the screen is thus completed.

Pinnotheres is a genus of crabs in which a resemblance to *Hapalocarcinus* might be expected, for its members live in similarly secluded positions, either the mantle cavity of molluscs or the tubes of worms; and both types of host being plankton feeders, they might be expected to share the diet. This does not appear to be the case and the oral appendages are very different. But the third maxilliped departs very considerably from the normal type. This is due to the fact that the abdomen has increased greatly in size, so that the buccal cavity has been correspondingly restricted, diminishing very greatly in depth. As a consequence the third maxillipeds are placed in a very different position, running almost at right angles to that which they occupy in other crabs. But they still form a double trapdoor, a little incomplete on the posterior border, where the deficiency is made up by a thick fringe of setæ. In the fusion of three joints of the endopodite of the third maxilla, *Pinnotheres* appears to differ from all other Brachyura.

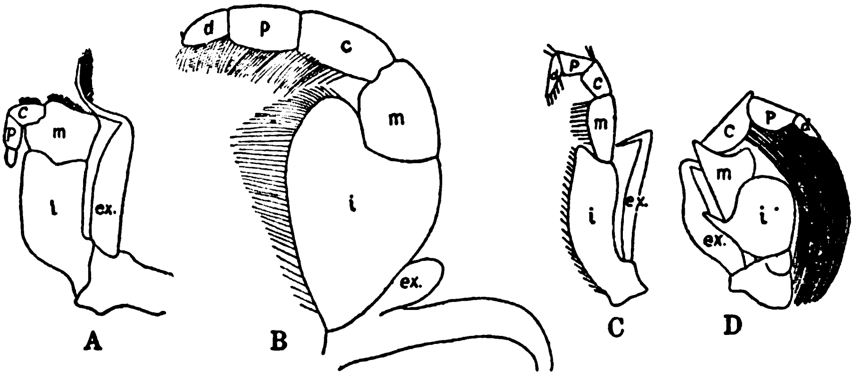

Fig. 6.—Various types of third maxilliped in the Brachyura.
A. *Cancer*, ×1. B. *Hapalocarcinus*, ×100. C. *Stenorhynchus*, ×4. D. *Porcellana*, ×6.
ex., exopodite; *i*, ischiopodite; *m*, meropodite; *c*, carpopodite; *p*, propodite; *d*, dactylopodite.

In *Ranina* among the *Anomura* a structure and disposition of the third maxillipeds are found similar to that occurring in *Stenorhynchus*. The basal articles of the endopodite are not enlarged, but the three last joints are bent down to fill in the gap and all are strongly setose. Curiously enough, when Milne Edwards described his genus *Lithoscaptes* (which is generally acknowledged to be synonymous with *Hapalocarcinus*) he compared the third maxilliped with that of *Ranina*. The only resemblance lies in the slender meropodite and the setose borders.

In *Hapalocarcinus* the arrangement of the buccal area is quite unique. It is very wide, so that the third maxillipeds are set far apart. The ischiopodite of the endopodite is rather broad, but the meropodite is no wider than the following joints. The last three are not bent posteriorly, as is usually the case, to aid in closing the buccal cavity, but are directed anteriorly and towards each other, while the setæ with which they are plentifully provided project internally. It will, then, be seen by reference to figure 9 that the buccal area is entirely uncovered and is only screened by a series of fringes of setæ borne successively by the endopodite of the third and the exopodites of the second and first maxillipeds. Together they form an efficient sieve. So far, then, from the buccal area being carefully guarded and closed lest the products of mastication should escape, free access is given to the mouth. The constant circulation of water is thus promoted and the mobile parts of the maxillipeds are given free play to separate out from the respiratory current those very minute organisms which form the food of *Hapalocarcinus.*

THE BUCCAL APPENDAGES.

The third maxillipeds have already been discussed in the last section. In text-figure 6 these appendages are shown in *Hapalocarcinus*, *Porcellana*, and *Stenorhynchus*. The peculiar feature of the appendage in the first genus is undoubtedly the rudimentary character of the exopodite, a feature not found elsewhere in the Decapoda Brachyura. Its absence is compensated for by the development of the distal joints of the endopodite, which instead of being turned backwards to form an insignificant trapdoor arrangement over the buccal area are comparatively stout and long, being directed inwards so that each meets its fellow of the other side, and with a much greater development of setæ than in other Brachyura. The ischiopodite is curiously shaped, it is true, but it still has a dilated form which in my opinion shows its descent from a Brachyuran stock in which the buccal area was broad and completely covered by the third maxilliped. The meropodite is slender, but so it is (and the ischiopodite as well) in *Stenorhynchus.*

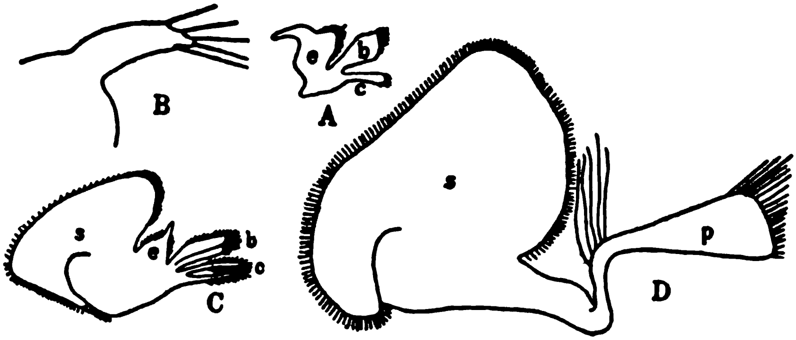

FIG. 7.—First maxilla of A, *Cancer*, ×1, B, *Hapalocarcinus*, ×70. Second maxilla of C, *Cancer*, ×1. D, *Hapalocarcinus* ×70; *b*, basipodite; *c*, coxopodite; *e*, endopodite; *p*, undivided protopodite; *s*, scaphognathite.

That which is significant is not that the endopodite has become slender, but that the appendages have been forced so far apart.

The *second* and *first maxillipeds* are fairly typical and call for no particular remark beyond the description of Calman.

The *second maxilla* consists firstly of a small triangular plate, the base of which is free and directed inwards, which represents the *protopodite*, not divided into a basipodite and coxopodite as in *Cancer* (where each again is bilobed). The inner border is provided with many setæ. Internally the appendage passes into a narrow neck, where a second bunch of setæ is given off and where a possible articulation occurs. Secondly, there is an *exopodite*, the *scaphognathite*, which attains the development usual in the Brachyura. The connection between the protopodite and the exopodite is very slender, thus differing from that in *Cancer* and other crabs. The protopodite subserves nutrition and its rudimentary character is thus strongly contrasted with the normal development of the exopodite, which performs a respiratory function. The partial disconnection of these two parts which appears to be in progress is perhaps due to the fact that their rhythmical movements do not coincide. The *endopodite*, found in other Brachyura, is wanting here.

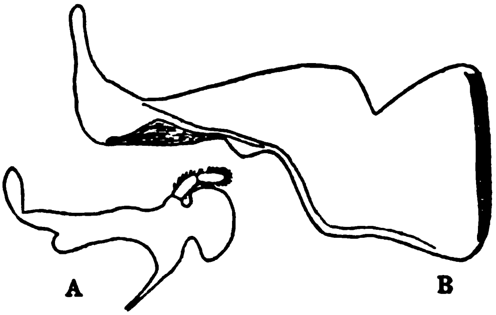

FIG. 8.—Mandible of A, *Cancer*, ×1; B, *Hapalocarcinus*, ×70.

The *first maxilla* shows a much greater reduction, since it is entirely masticatory in function. It is represented by a slightly curved, slender plate representing the protopodite. It is less than a quarter of the size of that of the second maxilla. It is undivided in contrast to the bilobed protopodite of other Brachyura. A few setæ are present internally. The endopodite is absent.

The *mandibles* are two smooth triangular plates, thin but more strongly chitinised than the other buccal appendages, with straight internal edges, not broad or much thickened, so as to serve for mastication, but capable of working over each other. Internally on each side is an apophysis for the attachment of the mandibular muscle. These appendages are evidently quite effective ones, though they are plainly not used for crushing organisms or food particles, as is usual in the Brachyura. Their operations may be confined to sifting or current creating. The absence of a palp is a very noticeable feature.

THE STOMACH.

The stomach of *Hapalocarcinus* differs distinctly from the type normally found in the Brachyura. In all the higher Crustacea the stomach is divided into two chambers, anterior or cardiac and posterior or pyloric. The cardiac chamber is a large spherical sac, the cuticle of which has been thickened locally to form a series of plates bearing teeth, the so-called *gastric mill*, an apparatus which continues the task, begun by the appendages, of breaking up the food into very small particles. The cardiac and pyloric cavities are partly separated by a valve which leaves only a narrow channel of communication and this, together with the anterior part of the pyloric cavity, is occupied by innumerable setæ springing from the unthickened cuticle and the ossicles. These form an effective sieve for preventing the passage of any but the smallest food particles into the mesenteron. In the posterior part of the pyloric region the chitin of the ventral wall is thickened to form the *pyloric ampullæ*, which consist of an elaborate arrangement of parallel ridges with rows of setæ springing between them, and constitute another filtering apparatus to which the food current is finally subjected.

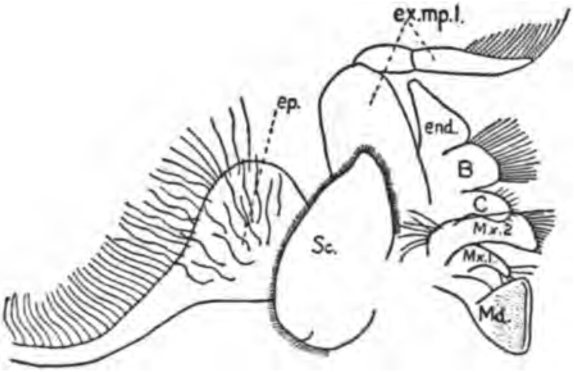

Fig. 9.—Buccal appendages of one side. ×90. First maxilliped, showing epipodite, *ep.*; exopodite *ex. mp. 1*; endopodite, *end.*; basipodite, *B*; and coxopodite *C.*, Second maxilla *Mx. 2*, and scaphognathite *Sc.* First maxilla, *Mx. 1*; mandible, *Md.*

In *Hapalocarcinus* this arrangement is very much simplified. In the cardiac chamber many of the plates have entirely disappeared and while the more important constituents of the gastric mill, the urocardiac and zygocardiac ossicles, are still present, they are much weaker and thinner and the teeth they bear, instead of being stout and blunt, are long and slender, passing into the setæ. Figure 11 shows, side by side, the zygocardiac ossicles, from *Hapalocarcinus* and from a very young and small *Carcinus* (not exceeding the first greatly in size). Their different nature and function will be readily appreciated. The remains of the gastric mill of *Hapalocarcinus*, no longer used in mastication, apparently aid the setæ of the pyloric valve in sieving the food current. At the same time it must be remembered that in other Brachyura the ossicles do sometimes give rise to occasional setæ; it is, however, usual to find them suppressed to form tubercles or fused to form teeth which are useful in the comminution of food. It is possible that to a large extent the formation of the plates of the gastric mill is due to the fusion of individual setæ, so that *Hapalocarcinus* has passed through a retrogressive process of evolution.

In accordance with the forward shifting of the sieving apparatus the structure of the pyloric chamber is very simple. The plates which are plentifully developed in other Brachyura are represented here only by one or two vestiges; sieves of setæ are almost entirely absent and the pyloric ampullæ which are so prominent a feature elsewhere are quite unrepresented.

As Mocquard states, in his comprehensive survey of the variations of the stomach in the Decapoda, numerous differences in the various groups and successive degradations are experienced, yet I have not been able to find in his descriptions and figures of Brachyura, or in such likely cases as I have myself examined, any in which the modification is so great as that occurring in *Hapalocarcinus*.

THE CONTENTS OF THE STOMACH.

It must of course be recognised that the stomach is very minute (about 0.5 mm. in breadth), so that it could not in any case contain very large fragments. But when I examined the stomachs of a dozen or so gall crabs, all but one appeared completely empty; in that one there were a few tiny representatives of the phytoplankton. This was in spite of the fact that the specimens were mounted after dehydrating without staining straight in Canada balsam and then examined with a $\frac{1}{12}$″ objective, so that even representatives of the nannoplankton should not have escaped notice.

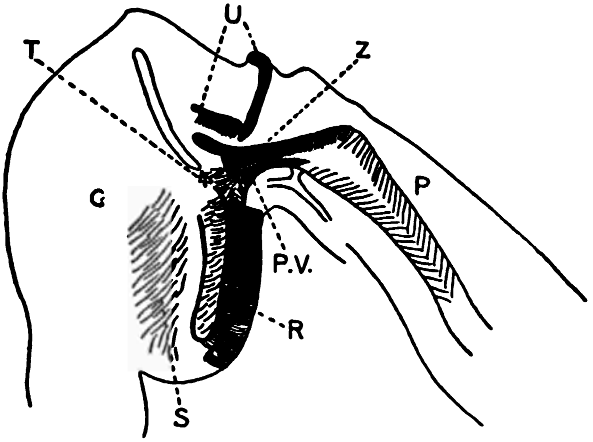

Fig. 10.—Stomach of *Hapalocarcinus*; side view. ×55.

C cardiac and *P* pyloric divisions of the stomach. *P. V.*, pyloric valve; *R*, alternating ridges and rows of setæ between, on the ventral wall of the stomach; *S*, setæ on lateral walls; *T*, a group of small tubercles; *U* urocardiac and *Z* zygocardiac ossicles.

This condition may be explained by a consideration of the probable course by which food reaches the mesenteron. In the first place, the food must consist of organisms contained in the currents of water drawn into the gall through the respiratory apertures. It is hardly necessary to repeat the statement of early observers that the crab does not devour the coral polyps. Moreover, the smaller members of the plankton alone can enter the gall (in the closed galls at least) and I have little doubt that the bulk of the food consists of the so-called "nannoplankton," which embraces all those animals and plants less than 3 to 4μ in diameter.

The currents of water drawn into the gall are of course caused by the action of the scaphognathite, for there does not appear to be any other mechanism of the calibre necessary for creating currents. The water used in respiration is, as is usual, drawn into the branchial cavity posteriorly and breathed out anteriorly. But the organisms contained in it, if not entirely prevented from entering the branchial cavity by the filter of setæ guarding the entrance, will at any rate partly be caught in eddies circulating under the ventral surface and probably in minor currents caused by the motion of the buccal appendages. The buccal area is so widened and the appendages so modified and dislocated that a maximum of water can circulate in the neighbourhood of the mouth.

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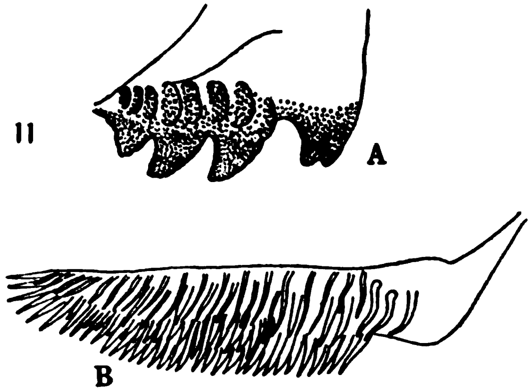

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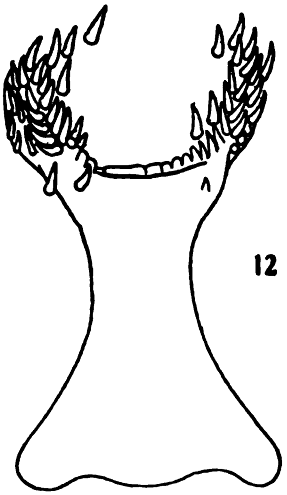

FIG. 11.—Zygocardiac ossicles of: A, *Carcinus*; B, *Hapalocarcinus*. ×220.
FIG. 12.—Urocardiac ossicle of *Hapalocarcinus*. ×220.

I suppose that the plankton is separated from the respiratory current by movements of the nets of setæ on the maxillipeds, resembling the sweeping action of the legs of Cirripedes. The smallest members of the plankton only, in view of the minute size of the apparatus, would be entrapped. They would then be sucked into the stomach by pulsating movements such as Mocquard has described in other Decapoda. He has shown that the stomach functions in the manner of a pump by the alternate action of the dilator and constrictor muscles. By the expansion of the cardiac sac the partially chewed food is sucked into the stomach and on its constriction the fluid taken in is expelled, while the solids are retained, largely owing to the action of the subœsophageal valve. It will be observed that notwithstanding the simplification of structure in the stomach of *Hapalocarcinus* there is still left the combination of ridges and fringes of setæ which occupy the posterior wall of the stomach between the cardio-pyloric valve and the œsophagus. These structures act as a filter to retain solid particles when water is expelled, but owing to the fact that these are all of small size no definite subœsophageal valve is present.

The food organisms which are thus taken into the cardiac chamber are all probably small enough to pass straight through the pyloric filter and chamber into the mesenteron, where they are digested; hence their customary absence from the cardiac chamber. This organ, though far too large for the requirements, has not been reduced in size since *Hapalocarcinus* acquired its present habits. The pyloric filter is preserved for the separation of occasional particles of larger size, but these must be rare, since they were never observed in the stomach. Almost certainly the crab must have the power of rejection of unsuitable pabulum.

Porcellana, amongst the Decapoda Anomura, obtains its food by a kind of net-fishing rather similar to that I have supposed occurs in *Hapalocarcinus*. The appendages are provided with very thick borders of hair, but particularly the third maxillipeds, on which they attain a considerable length, greater than that in the gall crab. Gosse has described the way in which *Porcellana platycheles* uses the third maxillipeds by making alternate casting movements "exactly in the manner of the fringed hand of a barnacle, of which both the organ and the action strongly reminded me." I examined the appendages and the contents of the stomach. In the former case little reduction is shown (the protopodites of both maxillæ are bilobed and the mandibles possess a palp), but the thickness and strength of the fringe of setæ, developed even on the mandibular palp, show that all the appendages are used for sifting and not for mastication. The stomach is usually fairly full of food, generally in small unrecognizable fragments, occasionally larger pieces of algæ. The proportion of planktonic organisms is not great and this is no doubt accounted for by the habitat of *Porcellana* under stones in littoral situations where the water is more usually muddy than clear, and organic débris abounds. So that while a similar method of obtaining the food is practised in both forms the nature of the food differs. In *Hapalocarcinus* it is much more minute and entirely in the form of living organisms.

It occurred to me that other of the higher Crustacea which had adopted a sedentary existence might have developed a similar dietary and alimentary apparatus. *Pinnotheres* lives within the depths of the mantle cavity of a mollusc or the tube of a worm. Its tiny chelæ, like those of *Hapalocarcinus*, show that it is in no sense a predatory animal. It might be expected that it would live on minute plankton like its host. If the size of the animal is to be taken into consideration, some species of this genus are not very much larger than the gall-forming crab. But on examination I found its stomach to be full of fragments, organic and inorganic, which showed a varied diet, and whose possible source was rather a puzzle to me. The walls of the stomach, moreover, showed a typical armature well fitted for mastication. The buccal appendages, though peculiar in some respects, showed little evidence of reduction in any way comparable to that in *Hapalocarcinus*.

Similarly, I examined the stomach of *Synalpheus brucei*, which I describe in another paper as a commensal with crinoids on the Pacific coral reefs, living for the most part if not entirely within the circle of their arms. It was in all cases crammed full of foraminifera, radiolaria, spicules of calcareous and siliceous sponges, and crustacean fragments, as well as pieces of coral skeleton. This examination showed how wide is the dietary of these quasi-sedentary creatures.

While no other member of the Decapoda shows similar modifications of the alimentary apparatus, there is a curious similarity between the oral appendages of *Hapalocarcinus* and those of an entire division of the lower Crustacea, the Branchiopoda. The following quotation from Sedgwick's Textbook of Zoology (Article Crustacea, by J. J. Lister, p. 369) summarises the conditions prevailing in the latter group:

> "It is remarkable that while the thoracic appendages of the Branchiopods conform so uniformly to a common and, as it appears, primitive type of structure, the appendages about the mouth present the greatest divergence from that type which is met with in any group of Crustacea. The absence of the mandibular palp in the adult is all the more striking because of its size and frequently biramous character in other Entomostracan groups, the Copepods and the Ostracods. Again the two pairs of maxillæ, which even in the Malacostraca conform more closely than any other appendage to the primitive 'phyllopod' type of limb, are here, in the Branchiopods themselves, perfectly simple lobes, and one pair is often missing. In adult Cladocera and in *Limnetis* among the Conchostraca there is only one pair; in *Branchipus* the second pair is rudimentary, and in this genus, as also in *Apus*, where two pairs are present, they are retarded in development, appearing later than the thoracic appendages which follow them in position. . . . The late appearance of the maxillæ is perhaps a confirmation of the view taken here that the simple condition of those appendages in the Branchiopods is a specialised and not a primitive character. The small size and simple character of the maxillæ is perhaps dependent on the peculiar habit of members of this genus . . . of passing the food forwards along the ventral groove."

The absence of the mandibular palp and the reduction of both pairs of maxillæ to a simple lobe are thus characters common to both the crab and the tiny Entomostracans. Lister concludes that this condition is secondary in the Branchiopoda and a similar conclusion with regard to *Hapalocarcinus* can not be avoided. Without doubt, also, the reduction in both cases is associated with particular habits of food collection, but the explanation in the last paragraph of the quotation is hardly adequate. A few remarks on the method of feeding in the Branchiopoda may be made before instituting a comparison with

Hapalocarcinus. A full account of the phenomenon has never been given, even for such common forms as *Daphnia* and *Simocephalus.* A short paper by Hartog and a few excellent observations by Woltereck comprise the sum of publication.

In such a form as *Daphnia* a current is constantly produced for respiration and feeding by the movement of the thoracic appendages. This current enters the space between the valves anteriorly and flows backwards ventrally; then turning upwards, comes in a reversed direction along the ventral groove to the mouth. The small organisms in it are collected beneath the labrum. The mandibles, which are palpless, unlike those of *Hapalocarcinus,* have a broad triturating surface covered by a number of longitudinal ridges beset with short processes. They are constantly in rhythmic motion, rubbing against each other and to enter the gut every particle must pass between them and be ground still finer. Mr. J. T. Saunders, of Christ College, Cambridge, has pointed out to me that the food of these creatures is the "nannoplankton" and Woltereck states that in his experience small algæ are the food supply. But, however minute the organisms on which *Daphnia* feeds may seem to be, they are subjected to a trituration which reduces them to an amorphous condition. The crushed fragments are then sucked in by the peristaltic action of the gut. In most animals the intestine is entirely filled with material in which it is difficult to detect any structure.

In briefly comparing, then, the feeding methods of *Hapalocarcinus* and *Daphnia* and the consequent effects upon structure, it must first be stated that both animals live on the smaller elements of the plankton, probably mostly the "nannoplankton." The reduction of the maxillæ in both forms is in some way associated with this fact. But there is a marked difference in the treatment of the diet; for while *Hapalocarcinus* possesses no effective organs of mastication, only preventing the access to the mesenteron of particles of too large a size by means of a sieve, *Daphnia* subjects every organism entering its small mouth to a thorough trituration by the very effective mandibles, appendages which differ entirely in structure from those of *Hapalocarcinus,* only agreeing, in fact, in the absence of a palp.

THE FEMALE AND ITS VARIOUS STAGES OF GROWTH.

The colouration of the living female has never been described before, so far as I know. In the younger females it is a light grey in gross effect. If examined with a good lens a great number of small yellow-brown spots are seen and between them branching white chromatophores. In the older females the grey is much intensified, so that the crab becomes the colour of lead.

When a crab is liberated from a gall it creeps about with surprising slowness. If a branch of coral be offered it, it clings to it with the closest embrace and makes its way very slowly over the surface in search of a hole. The legs, though rather weak, are provided with sharp claws which it sticks into the cœnosarc of the colony. If several crabs are contained in the same vessel they come together and fight vigorously (though under natural conditions they can have no opportunity of satisfying these proclivities). It is clear that the crab is strongly thigmotropic, a property developed in correlation with its secluded life.

It is first my intention to give an explanatory description of the series of females which are illustrated here. As was stated in the preliminary description, the crab settles down when it is immature. The youngest females, found in galls consisting solely of the chamber *A*, have a carapace length of 1.5 to 1.75 mm. and their sex is hardly recognisable. They have a narrow abdomen with no trace of swimmerets; there are no reproductive apertures and the genital gland has not developed. But there is equally no sign of male characters and a perfect gradation exists between these apparently sexless forms and the adult female. This youngest female I denote as Stage I.

In Stage II, though the abdomen is very little broader, rudiments of the swimmerets appear and also the female apertures on the sternum opposite the third thoracic legs. The carapace length is 2.0 mm.

In Stage III the abdomen is definitely broader, though only in segments 4, 5, and 6. The rudiments of the appendages are rather longer and the first pair show indications of bifurcation. The carapace length is 2.5 mm.

In Stage IV all the abdominal segments except the last have shared in the increase of breadth. The carapace length is 3 mm.

Stage V shows further broadening of the abdomen. The carapace length is 3.2 mm.

In Stage VI the abdomen is almost as broad as the carapace. It will be seen that the hypertrophy is due to the growth of the last three segments. The ovary is well developed in the cephalothorax. The carapace length in the specimens figured is 3.5 mm. This appears to be the same stage as that described and figured by Calman (l. c., pl. 3, figs. 29, 30), but he gives the carapace length as 2.6 mm., which is very much smaller than that in mine.

In Stage VII the abdomen is wider than the carapace, the last three segments being greatly widened to form a pouch. In nearly all these, eggs are found attached to the appendages. The two stages figured here show that marked growth takes place even after reproduction commences. This may be estimated from the following figures:

	Stage VI *a*.	Stage VI *b*.
Carapace length....................	4.5 mm.	5.2 mm.
Total length........................	7.5 mm.	8.5 mm. to 9.0 mm.
Breadth of carapace................	4.0 mm.	5.0 mm.
Greatest total breadth (abdomen)....	....	9.5 mm. to 10.0 mm.

As can be seen from figure 10, the ovary invades the abdomen to a great extent. The great size of the abdomen is perhaps best appreciated in a side view (fig. 9).

By the time that Stage VII has been reached the gall is almost closed. Fertilisation takes place when this stage is reached (see next section). After closure of the gall the male is unable to pay further visits, so fertilisation must be confined to a brief period and may occur only once. But the spermatozoa must retain their vitality for a long time within the spermathecæ, for oviposition proceeds until the gall crab dies, and a large number of successive broods are probably produced.

THE MALE.

I have mentioned above the fact that the male of *Hapalocarcinus* has remained unknown up till the present, and have quoted Calman's conjecture that the sexes both become mature during a free-living phase and that after impregnation the female settles down and forms a gall in which she is imprisoned. I was myself at first inclined to believe that in *Hapalocarcinus* we had another example of protandric hermaphroditism, like *Lysmata seticaudata*, described by Spitschakoff.* This seemed to be indicated by the male-like appearance of the youngest inhabitants of galls with their narrow abdomens. But the absence of male apertures and copulatory styles supported the alternative supposition that they were immature females. For some time, then, I was unable to find an undoubted male, though I examined as many as a hundred galls. But at length, on examining one which was just closing, I found it occupied by a female (Stage VI) with her recently moulted skin and a much smaller individual of about 1 mm. carapace length. This was identified as a male on account of the well-developed and typical copulatory styles and a pair of enormous testes full of mature spermatozoa, which appeared as opaque white structures in the cephalothorax. From this discovery, which I confess was never repeated, I conclude that the male is normally very much smaller than the adult female and not even so large as the young immature females which are found in the least-developed galls; also that he is free-living and visits the females within the galls, copulation taking place at a period when the gall is still open, but the ovary of the female is already well grown. As in the other Brachyura, so here it only occurs just after the female has moulted. Soon after a stock of sperm has thus been secured the gall closes up, so that the visits of other males are barred. But the female begins to lay eggs and lays apparently brood after brood, which develop within the ample shelter of the abdomen until they reach the zoæa stage. Then the larvæ are liberated to the exterior through the tiny circular outlets of the gall.

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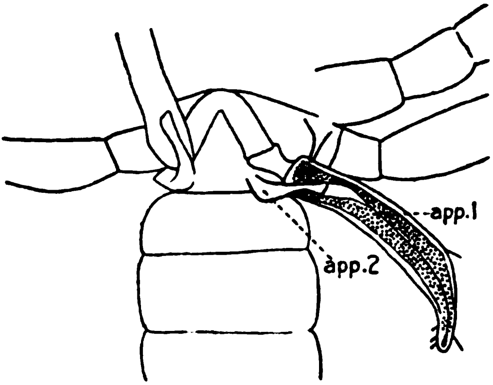
*Zeit. wiss. Zool., Bd. 100, p. 190, 1912.

The male is figured in the ventral and dorsaal spects where, though it is so small, it will be seen that none of its organs show any signs of degeneracy. This is so for the internal as well as the external organs. The alimentary canal is apparently quite normal; the buccal appendages resemble almost exactly those of the female. Yet it will be seen that the reproductive organs reach a remarkable state of development. The opaque white structures which I have referred to above occupy a large part of the dorsal surface of the cephalothorax. The fact that they are full of mature spermatozoa leads one to regard them as vesiculæ seminales rather than testes and it is difficult to recognise in them the tubular shape of the testes and vasa deferentia of the Decapoda generally. A noticeable point is that the spermatozoa all lie free in vesicula seminalis and are not contained in spermatophores. The absence of tubular testes at the time of examination is probably due to the fact that the male is short-lived and spermatogenesis is confined to a short period, during which all the germ cells are rapidly used up and enormous numbers of spermatozoa are produced.



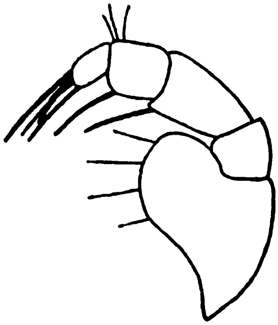


Fig. 13.—Copulatory appendages of male of *Hapalocarcinus*. × 50. *app. 1*, first abdominal appendage; *app. 2*, second abdominal appendage.

Fig. 14.—Third maxilliped of male *Hapalocarcinus*. × 80, to show the small number of setæ fringing the inner border.

The spermatozoa are very tiny discs about 5 μ in diameter. They are without marginal processes.

In the female, spermatozoa are found in the spermathecæ, which are rather large, rounded sacs in the ventral part of the body cavity, just at the female openings. They are exactly like those seen in the vesiculæ seminales, but are cemented together evidently by a substance secreted by the spermathecal epithelium.

As is usual in the Brachyura, the appendages on each side of the first two abdominal segments unite to form a single copulatory organ. The anterior appendage is tubular; its cavity is large at the base, but soon diminishes greatly and only widens again at the tip where it opens.

This tip is not attenuated, as in most crabs, but is comparatively broad and rounded and bears several small setæ. The posterior appendage is much shorter and is inserted in the basal cavity of the anterior appendage. Its apex is broad, not stylet-like, as, for instance, in *Cancer*. The generally accepted function is that of forcing the spermatozoa into the spermatheca of the female by working up and down in the cavity of the anterior appendage when the copulatory organ is introduced into the vulva of the female, and its piston-like structure would indicate this here.

I have not observed *genital papillæ*.

The great length of life in Arthropod spermatozoa is of course well known. The case most often quoted is the bee, where the queen is only once fertilised. In the other Brachyura it is said that the spermatozoa "remain inside the spermatheca for many months before they fertilise the ova." (I quote from Pearson.)

THE EGGS AND LARVÆ.

The eggs of *Hapalocarcinus* are quite large in size and heavily yolked. I never observed the larvæ hatching, but a great many of the individuals collected bore larvæ very nearly ready to be set free. They are then in the zoæa stage, with very distinct frontal, dorsal, and lateral spines, and large paired eyes in the head. All the head appendages are developed and the first two maxillipeds, large biramous structures, in the thorax. The segments of the abdomen are quite distinct and there is a forked telson. It seems, then, that this stage corresponds to the first zoæa stage of *Cancer* (Pearson) and thus hatching takes place here at a slightly later stage. The great difference between the protozoæa (the hatching stage in *Cancer*) and the first zoæa is the presence of the frontal and dorsal spines. The protozoæa is apparently omitted from the life-history of *Hapalocarcinus*.

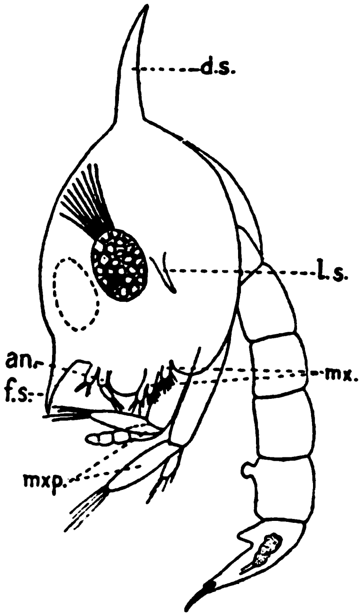


Fig. 15.—Zoæa larva of *Hapalocarcinus*. × 90.

***d.s.*, *l.s.*, *f.s.*, dorsal, lateral, and frontal spines.**
***an.*, first and second antennæ.**
***mx.*, first and second maxillæ.**
***mxp.*, first and second maxillipeds.**

The spines of the carapace are less prominent than in *Cancer*. The dorsal spine is longest. The first antenna is short and stumpy; the second antenna is very short but biramous. The mandible is visible as a not very definite plate.

CRYPTOCHIRUS Heller.

Cryptochirus is a genus described by Heller in 1872 from the Red Sea and associated by Calman with *Hapalocarcinus* to form the family Hapalocarcinidæ. Heller was not able to impart much information about the biology of the crab, but he gives an accurate account of the structure, even to the minute oral appendages, accompanied by figures which are helpful if hardly adequate according to present standards.

Semper was the first to supply first-hand observations of the living animal which he found inhabiting various Astræid corals in the Philippines. He discusses the interaction of crab and coral polyps in a passage which I will quote in full.

Semper first states that the influence of the respiratory current of *Cryptochirus* is exerted in quite a different way to that of *Hapalocarcinus*. This is due to the fact that the former genus only inhabits the more massive forms of coral and consequently the cavities in which it lives are unlike those in which *Hapalocarcinus* is found:

> "Here there are no galls, but merely cylindrical or funnel-shaped hollows, which are never closed during the lifetime of the crab, so that it certainly would be able to quit its position. Nevertheless, it as certainly does not do so; but the species I observed living thrust the forepart of their bodies very far out of their peculiar 'cave dwellings,' so that only their pouches, *i. e.*, the hind part of the body, remained within. The cavity itself exhibits some remarkable peculiarities. The bottom of it, on which the pouch rests when the creature has completely withdrawn itself into it, displays the radial septa of a polyp-cup one above another. They there are perfectly distinct, while the side walls of the cylindrical cavity are so completely lined with a thin calcareous crust that nothing can be seen of the perpendicular septa of the polyp-cup. From this it is evident that the young crab, or the larva of it, takes up its abode in the centre of a cup, and so kills the polyp inhabiting it. A specimen now lying before me, with an incomplete cave-dwelling, shows that the crab grows at first at the same rate as the surrounding polyps; for the margin of the crab's hole, which is perfectly cylindrical, is on exactly the same level as the neighbouring cups, and its breadth too is exactly the same. The cavity is six millimètres long, and the length of the crab found in it exactly corresponds. In another example, however, the length of the pit is twenty millimètres, while that of the crab belonging to it is not more than seven millimètres, at any rate in the dried state. This proves that the crab ceases to grow much sooner than the coral; and this conclusion is strikingly confirmed by the fact that the margin of the cylindrical pit is not on the same level as that of the surrounding polyp-cups, but much deeper. From the margin of the crab's dwelling, properly so called, there is a funnel that widens to the top, and of which the margin, as is shown in the cut (fig. 68), is gradually merged in the upper prominences of the coral. The crab living in the funnel thus formed was carefully observed by me during a long period of its life, and I was enabled to see that it protruded itself far enough out of its hole to be able to reach with its outstretched fore-claws almost to the highest portion of the funnel.
>
> "The whole conditions here described allow of no other explanation than the following: At first the crab and the coral grow at an equal rate; for, if the

> coral grew more rapidly than the crab, an inverted funnel or hollow cone would be formed over the crab, while, if the crab grew the faster, the margin of its cave-dwelling, so long as it was small, could not be exactly on a level with the margin of the contiguous polyp-cups. But when the crab has reached its full length, about seven millimètres, the polyps outgrow its funnel-shaped dwelling, and would no doubt soon wholly outgrow it, if it were not that they find a certain resistance in the current set up by the crab for breathing and in the movements of the creature; and this resistance is sufficient to compel the growth of the coral in a particular and determined direction. The two powers in opposition thus reach an equilibrium, and it is their reciprocal action which gives the funnel its characteristic form.
>
> "Here too, as in the former instance [*Hapalocarcinus*], the individual polyps plainly show the effects of the current. While in general the cups are perpendicular to the surface of the coral, in most of those which grow within the funnel this is not the case; they have an oblique direction upwards, and are most oblique where the strength of the current is greatest, *i. e.*, at the narrow bottom part of the funnel."

The material I have investigated comes from Minikoi and has already been reported upon by Borradaile (Fauna and Geography of the Maldives and Laccadive Archipelago, vol. I, p. 271, Marine Crustaceans, III, Xanthidæ and some other crabs) and referred to the species *Cryptochirus coralliodytes* Heller. They were collected by Professor J. Stanley Gardiner and are preserved in the Cambridge University Museum of Zoology. There were three males and several females. The dimensions (in millimetres) were as follows:

	Largest female.	Smallest female.	Largest male.	Smallest male.
Total length.........	8	....	....	....
Carapace length......	4	2.7	3	2.7
Carapace breadth....	3	1.6	1.7	1.5

These measurements are very similar to those given by Heller for *C. coralliodytes* from the Red Sea.

The notes given by Professor Gardiner are as follows:

> "A block of *Leptoria tenuis*, which had a large number of round holes on the surface up to 4 mm. across, was broken up. The holes . . . were nearly all found to be occupied by a symbiotic crab. The holes varied in depth from 1 to 30 mm., the coral being in the latter case 48 mm. thick. Normally the animal would appear to live close to the surface, with the carapace as a kind of shield closing the hole. When the block becomes more or less dry they retreat into the bottom of the holes. . . . These commensals are extremely common in *Leptoria* from the lagoon at Minikoi, but are never found in specimens from the outer reef. They are rare on other corals, occasionally in massive Astræids from the lagoon at Minikoi, but not apparently in branching corals, fungoids, or perforate corals."

I examined a number of colonies in a dried condition from the collections of Professor Stanley Gardiner and Mr. Cyril Crossland. In a spherical colony of *Leptastræa solida*, about 4 cm. in diameter, from Minikoi, there were six pits occupied by dried *Cryptochirus* and a large number of others which resembled the first exactly and so were probably once occupied by crabs. Each pit is cylindrical and uniform in diameter. At the bottom are to be seen the septa and columella of a dead polyp; the walls are perfectly smooth. The depth only varies from 4.5 to 5 mm. and in all cases the inhabitants were barely mature females. It seems, then, that all these symbiotic crabs had established themselves simultaneously or practically so, no very long time ago.

In a fragment of a colony of *Leptoria tenuis* (plate 3) also from Minikoi, and so possibly the very specimen alluded to in Professor Gardiner's account, there were three deep pits measuring respectively 12, 16, and 40 millimetres with a regularly circular cross-section. In the first of these was a female *Cryptochirus* with well-developed abdomen (but not bearing developing eggs) much larger than those found in the colony described above. There was also a shallow pit only 3 mm. deep which contained a male. This observation is of great interest. In *Hapalocarcinus* it is fairly certain that the male never forms galls, but leads a short and wandering life. In *Cryptochirus dimorphus*, where the male is very much smaller than the female, a pair is found in each pit according to Henderson (4), the male nearly always adherent to the female. In this species, then, it may be assumed with certainty that the female is the original householder and that the male is a mere lodger benefiting by the hospitality of the other sex. But in *Cryptochirus coralliodytes*, where the disparity in size is not so great, as far as my limited experience goes, solitary females usually inhabit the pits, but sometimes the males form and tenant very shallow ones, so that separate establishments for the sexes is the rule. But the shallowness of the pits containing males shows that they are short-lived or given to changing their residence. The structure of the males, moreover, is not so much adapted for life in a deep pit as is that of the females. The walking legs of the second pair are not stronger than the others and the swollen chelæ are not fitted to assist in scrambling up and down a smooth-walled hole. It is obvious that both sexes must leave their holes at certain times. The female fits so tightly in her hole that she must come to the surface of the coral colony to moult, and so there copulation also will occur.

It seems, then, from the information we at present possess, that the three species described in the family present an interesting gradation in sexual habit. In *Hapalocarcinus marsupialis* the male wanders about from gall to gall and is very short-lived; in *Cryptochirus dimorphus* he lives a sedentary existence, but merely as a commensal of the female crab; while in *C. coralliodytes* he actually forms a house of his own, where he maintains an independent position.

A COMPARISON OF HAPALOCARCINUS AND CRYPTOCHIRUS.

There is no doubt that *Hapalocarcinus* and *Cryptochirus* are very closely related. The same striking modifications of structure occur in both. Of these the reduction of the oral appendages and the gastric mill show a common method of feeding, while the abnormal growth of the abdomen is connected with the production of large broods of eggs, a property very necessary for a sedentary animal. The structure of the oral appendages and the maxillipeds is almost identical in the two cases (text-figure 16). The abdominal appendages, also, have exactly the same modifications.

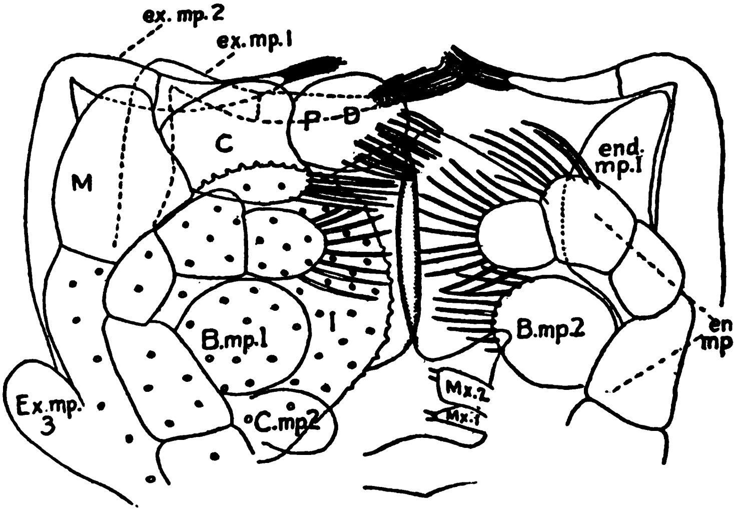
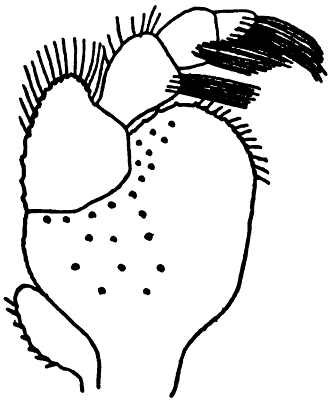


FIG. 16.—Buccal area of *Cryptochirus*. × 90.

For comparison with that of *Hapalocarcinus*. Drawn from a specimen cleared in potash and mounted in Canada balsam. On one side maxilliped 3 and parts of other appendages have been removed; on the other maxillipeds 1 and 2 are shown occurring beneath 3. The papillæ on the surface of maxilliped 3 are indicated by small circles. It will be seen that maxilliped 3 comes much closer to the middle line than in *Hapalocarcinus* and that the provision of setæ for the exopodites of maxillipeds 1 and 2 is not marked, while they are not found on the border of maxilliped 3. The main work of sieving is done by the strong setæ arising from the endopodites of maxillipeds 2 and 3. The sieve has not so fine a mesh as in *Hapalocarcinus*.

B. mp. 1, *C. mp. 2*, basipodite and coxopodite of first maxilliped; *mx. 1*, *mx. 2*, first and second maxillæ. Other letters as in text-figure 5.

Such structural differences as exist correspond to their diverse habitations. *Hapalocarcinus* affects branching corals with individual polyps much smaller than itself, even at the earliest stage, and forms a complicated gall almost completely shut off from the exterior by controlling and modifying the branching of the coral. *Cryptochirus*, on the other hand, seeks to house itself in massive Astræid corals, where the individual thecæ are of such size as to accommodate the intruder. It occupies a theca after passing through its larval stages and very soon the growth of the polyp is suppressed and death will follow. The growth of the polyps around it continues, but the mere mechanical effect of the presence of the crab causes a circular pit to be left, whose depth gives the amount of growth of the colony since the crab first settled down. This pit is almost uniform in diameter, since the growth of the crab is in length and hardly at all in breadth; and it is circular in section, this being the shape of the original theca, to which *Cryptochirus* speedily adapts itself. The depth, size, and shape of the house are thus primarily dependent on the polyp and its manner of growth. These characters are not determined by the crab in anything like the manner in which *Hapalocarcinus* affects those of the gall. Moreover, the shape of the pit is responsible for the form of its inhabitant and not *vice versa*. Thus, to occupy the circular pit the cephalothorax of *Cryptochirus* has become uniformly cylindrical; the soft abdomen easily adapts itself to the same shape. In order that the creature may raise itself easily and quickly in its long tube and retire to the bottom with equal speed, the four posterior pairs of walking legs are very strong and furnished with very sharp claws to obtain a purchase on the smooth walls of the pit. They are also flattened from side to side, so as to work more easily in the confined space.



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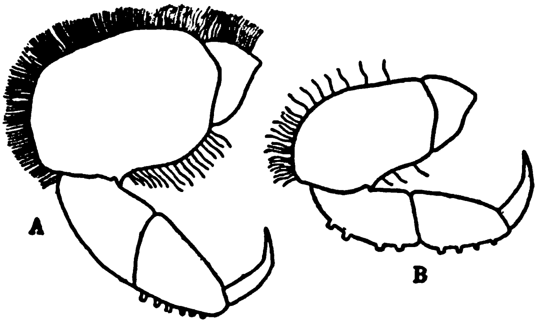

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FIG. 17.—*Cryptochirus coralliodytes*. Third maxilliped. × 50. Compare with that of *Hapalocarcinus* in text-figure 5 C. The surface of the ischiopodite is papillated.

FIG. 18.—× 25. A, second pair of thoracic legs, to show the great development of the flattened meropodite. B, third pair of thoracic legs.

The carapace of the crab is humpbacked, its anterior surface forming a thickened disc placed obliquely to the rest. Such a view as that in figure 19 A, shows the mouth of the pit largely filled up by this anterior part of the cephalothorax, while to the sides and in front the chelæ and especially the second pair of walking legs help to close the entrance and also to maintain the crab in its position at the mouth of the hole. So here, as in all tubicolous animals, a sort of operculum is formed which closes the mouth of the tube and protects the soft posterior parts from injury.

The female has the second pair of walking legs rather longer and much stronger than the rest. The femoral article in particular is strongly compressed and very broad. In fact, the lateral view of the female crab reminds one greatly of the burrowing Orthopteran insect *Gryllotalpa* with its stout strong first pair of legs modified for burrowing. Heller, in 1862, also called attention to the resemblance in general shape to the cylindrical wood-boring beetles. But *Cryptochirus* differs from both these cases in the fact that no active boring and burrowing is performed and the great development of one pair of appendages in both *Cryptochirus* and *Gryllotalpa* is thus due to different causes.

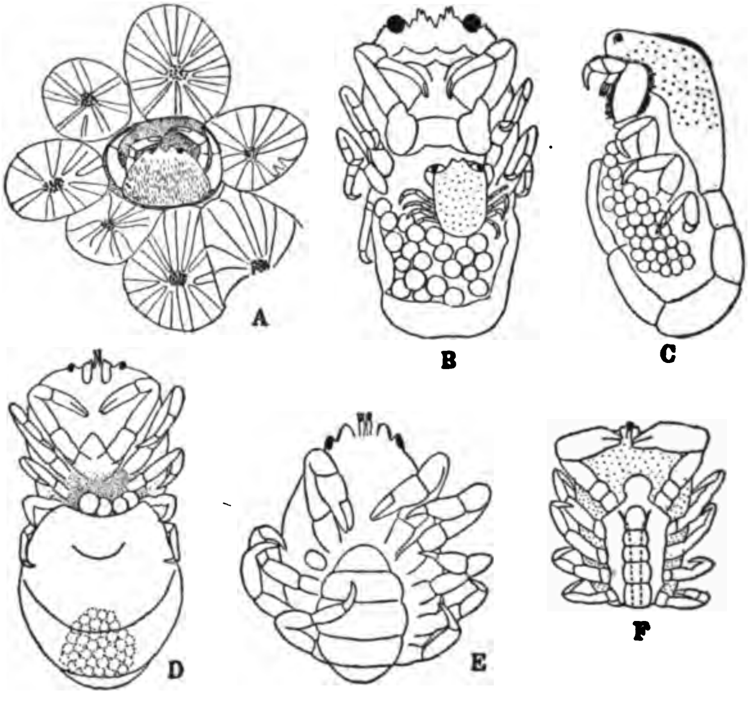

FIG. 19.

A. *Cryptochirus coralliodytes* in its natural position in a colony of *Leptastræa roissyana*. The crab is seen in its pit, the cup of a dead polyp, surrounded by normal polyps. It will be noticed that the only part of the carapace visible is the obliquely flattened anterior part; the chelæ and the second pair of thoracic limbs fill up the space to the sides. This illustration does not convey quite adequately the effective way in which the pit is filled up by its inhabitant.

B. *C. dimorphus* (after Henderson). Female and male, ×8, to show the striking sexual dimorphism in this species. Compare with figures D and F of *C. coralliodytes*, where the male and female are drawn to the same scale and are more nearly the same size.

C–F refer to *C. coralliodytes*.

C. Side view of mature female, ×6. The eggs in the brood pouch are indicated as seen through the transparent lateral walls of the latter. Note also the flattened anterior part of the carapace, and the enlarged second pair of thoracic appendages used in movement in the pit.

D. Ventral view of mature female, ×6. Some of the developing eggs in the brood pouch are seen projecting from it. The immature eggs in the ovary are indicated by the dotted circles in the abdomen, posteriorly.

E. Immature female, ventral view. To show narrow abdomen.

F. Male, ×6, to show size compared to mature female. The copulatory styles are represented by dotted lines passing beneath the abdomen, emerging at its anterior end.

THE AFFINITIES OF THE HAPALOCARCINIDÆ.

On this subject Calman writes as follows:

> "While the characters of *Hapalocarcinus*, as now described, show clearly that it must stand alongside *Cryptochirus*, they give little help towards settling the place of the two genera in the system. The position of the female genital apertures shows that they must be placed among the true Brachyura, although there are some curious resemblances to individual genera of the Anomura. Thus the endopod of the third maxillipeds resembles somewhat that of *Porcellana*, while the rudimentary exopod suggests a comparison with the Hippidea. The number and uniramous condition of the abdominal appendages also agree, except for the absence of the sixth pair, with the last-named group. These resemblances, however, are balanced by numerous important differences, so that even were we to set aside the evidence of the genital openings it would be impossible to place the genera in any of the groups of Anomura. On the other hand, the characters of the third maxillipeds and of the abdominal appendages and the greatly enlarged buccal area are unlike anything found among the Brachyura. The resemblance to the Pinnotheridæ appears to be quite superficial."

My own opinion coincides almost exactly with that of Calman, but I am inclined to lay even less stress on the resemblances to the Anomura. The characters of the male are typically Brachyuran. The likeness between the third maxillipeds of *Porcellana* and *Hapalocarcinus* is due to a similar mode of feeding. I have dealt at length with two of the divergences from the Brachyuran type mentioned by Calman; and the third, the character of the abdominal appendages, is more nearly paralleled by *Pinnotheres* amongst the Brachyura than by the Hippidea, as Calman suggests. But in spite of this fact I thoroughly agree that there is no near relationship between *Hapalocarcinus* and *Pinnotheres*. Calman says further with regard to this point:

> "In describing *Hapalocarcinus*, Stimpson noted its resemblance to *Pinnotheres* in the large size of the abdomen and the softness of the integument, and he stated that its systematic position was probably between *Pinnotheres* and *Hymenosoma*. Apart from the two points mentioned, there seems to be little in the characteristics of the species as now described to suggest affinity with the Pinnotheridæ, while the third maxillipeds are widely different in type from anything found in that group."

In *Hapalocarcinus* ♀ there are three pairs of abdominal appendages, while *Pinnotheres* ♀ possesses the normal number, four. There is, however, in both a tendency to a complete suppression of the exopod, a tendency not exhibited in other Brachyura, so far as I know.

The following statement of the appendages forms the basis for a more exact comparison:

Segment.	Hapalocarcinus.	Pinnotheres.
1.......	....	....
2.......	Biramous, but exopod rudimentary...	Biramous, but exopod rudimentary.
3.......	Uniramous........................	Biramous; exopod very well developed.
4.......	Uniramous........................	Uniramous.
5.......	....	Uniramous.

Cryptochirus is like *Hapalocarcinus*, but the rudimentary exopod is not present in the appendage of the second segment. It must also be noted that in the third maxilliped the ischiopodite and the meropodite are more expanded than in the latter genus. The third maxilliped of *Cryptochirus* thus forms more of an operculum for the buccal region than it does in its relative. The sieve mechanism (text-figure 16) is also less developed, and altogether it can hardly be said to be so highly modified as in the gall-forming crab; this is no doubt due to the fact that isolation in the gall and consequently a preliminary filtering of the plankton at the gall apertures make it necessary to have as perfect an apparatus as possible.

THE HOSTS OF HAPALOCARCINUS AND CRYPTOCHIRUS.

The names in brackets are those of the authors responsible for the record.

(1) *Hapalocarcinus marsupialis* Stimpson.
  Pocillopora:
    P. cæspitosa Dana [Verrill, Hawaiian Islands; Potts, Murray Island]; ? *P. brevicornis* Lam., *P. elongata* [Verrill, Ceylon]; *P.* sp. [Semper and D. Graeffe, quoted by Semper].
  Seriatopora:
    S. hystrix [Semper, Philippines; Potts, Murray Island]; *S. imbricata* [Bassett-Smith, China Seas]; *S. elegans* ? probably identical with *S. hystrix* [Calman, Murray Island].
  Sideropora:
    S. palmata, *S. digitata*, [Semper, Philippines].
  Stylophora:
    S. raristella Dep. var *wilsoni* J. S. Gard. [Potts].
  Hapalocarcinus has also been recorded from *Millepora* by Hickson.
(2) *Cryptochirus* Heller.
  C. coralliodytes Heller:
    Goniastræa bournoni; Astræa sp., *Trachyphyllia* sp. [Semper, Philippines]; *Trachyphyllia* sp. [A. Agassiz, quoted by Semper, West Indies]; *Leptastræa solida* (Ed. and H.); *Leptoria tenuis*, [Potts, Minikoi]; *Hydnophora lobata* [Potts, Port Sudan, Red Sea.]
  C. dimorphus Henderson. In "a large branching madrepore."

SUMMARY.

Hapalocarcinus.

(1) The stages in the formation of galls in colonies of *Pocillopora* and *Seriatopora* are here fully described.

(2) The *male*, here described for the first time, is found in open galls with females which have just reached maturity. It is rather smaller than the youngest female here described.

(3) The *females* vary in size, from very small individuals with narrow abdomen without appendages, gonads and generative apertures not having been yet formed, to large forms with hypertrophied abdomens forming brood pouches laden with developing eggs. The galls correspond in development to their inhabitants.

(4) The peculiarities of the buccal appendages and the reduction of the armature of the stomach are explained by supposing that the crabs live on the nannoplankton drawn into the galls with the respiratory current. This is supported by the fact that the stomach is always apparently empty, closer examination sometimes showing very minute organisms.

Cryptochirus.

(5) In *Cryptochirus coralliodytes* the male does sometimes form shallow pits and does not inhabit the same pit as the female.

(6) The sexual dimorphism in this species is much less marked than in *C. dimorphus.*

(7) Buccal appendages and stomach exhibit the modifications found in *Hapalocarcinus* and a similar method of feeding is probably employed.

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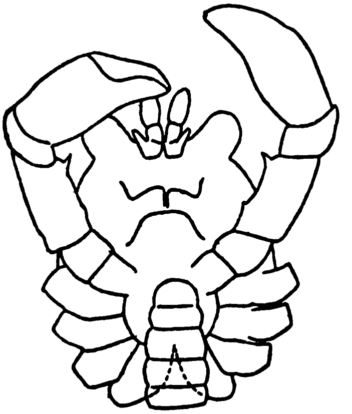

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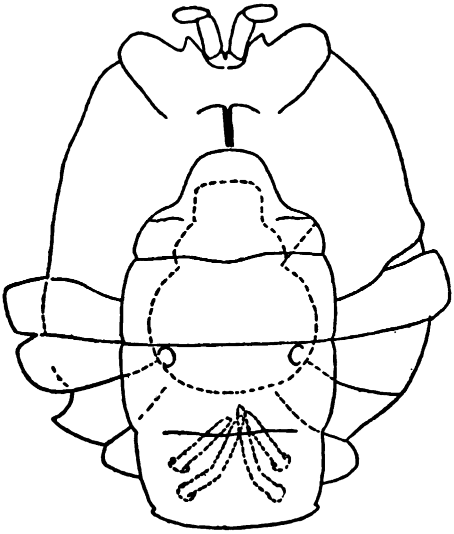

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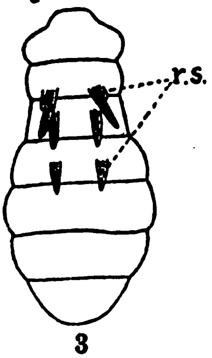

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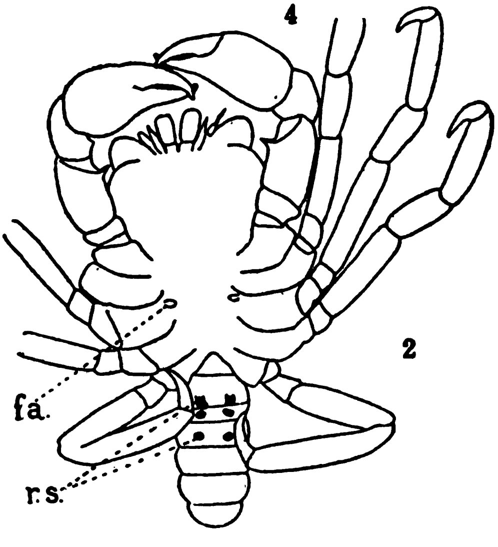

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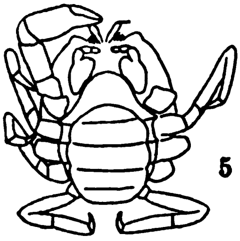

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Hapalocarcinus marsupialis. Female.

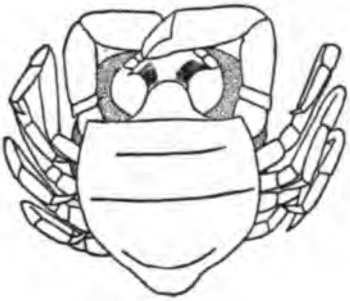
Fig. 1.—Stage I. Ventral view. Narrow abdomen and no reproductive apertures. Carapace length, 1.75 mm. × 18.

Fig. 2.—Stage II. Ventral view. Abdomen reflexed to show rudiments of the three pairs of appendages. Female apertures developed. *fa.*, position of the generative apertures; *r. s.*, rudimentary appendages of the abdomen. Carapace length, 2.0 mm. × 18.

Fig. 3.—Stage III. Ventral view of abdomen only. × 18.

Fig. 4.—Stage IV. Ventral view of individual boiled in caustic potash and mounted in Canada balsam so that the female apertures and the abdominal appendages can be seen underneath the abdomen. Carapace length 3.0 mm. × 18.

Fig. 5.—Stage V. Ventral view. × 8.



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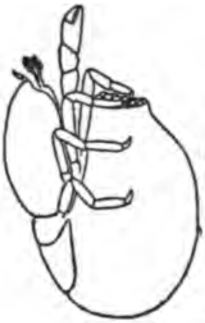

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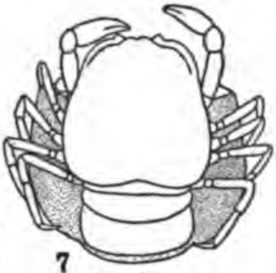

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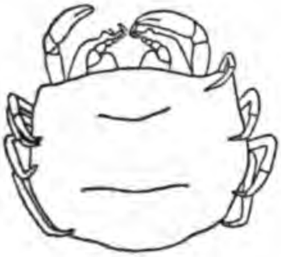

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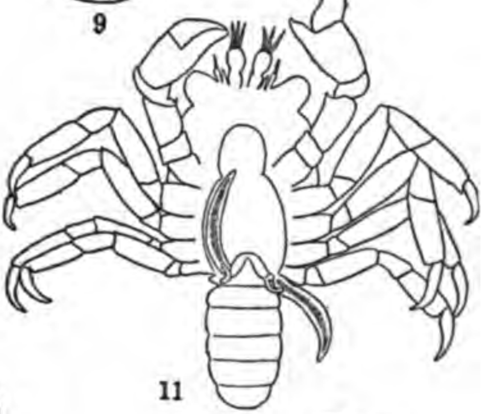

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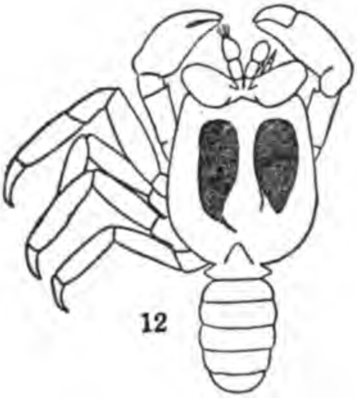

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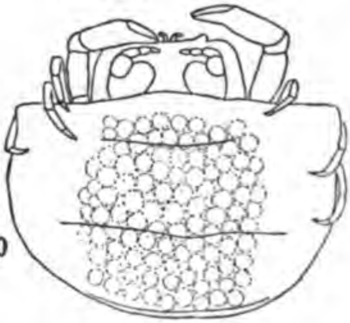

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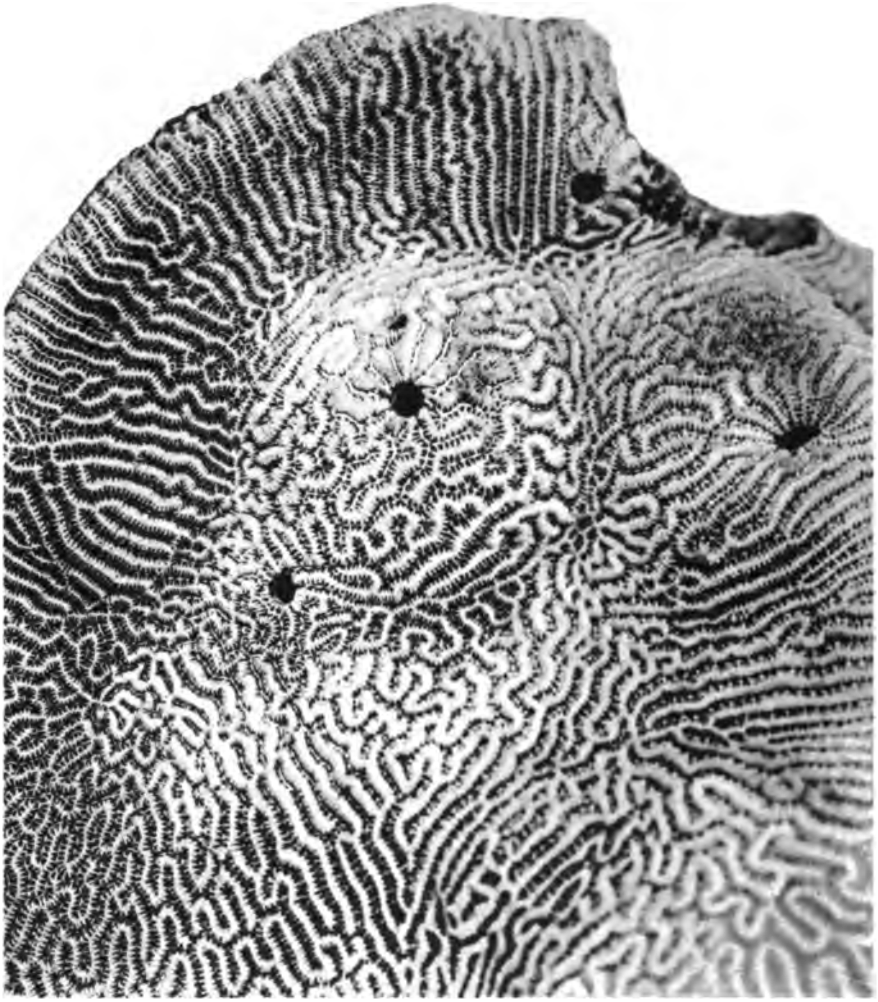
Hapalocarcinus marsupialis.

Fig. 6.—Female, stage VI. Ventral view. ×8.
Fig. 7.—Female, stage VII*a*. Dorsal view. ×4.
Fig. 8.—Female, stage VII*a*. Ventral view. ×4.
Fig. 9.—Female, stage VII*a*. Lateral view. ×4.
Fig. 10.—Female, stage VII*b*. Ventral view. ×4. The dotted circles indicate eggs seen through the semi-transparent abdomen.
Fig. 11.—Male, Ventral view, showing copulatory stylets. ×18.
Fig. 12.—Male, Dorsal view, showing vasa deferentia. ×18.



Pits of Cryptochirus coralliodytes in a colony of Leptoria tenuis from Minikoi. About natural size. From a photograph of a specimen now in the Cambridge University Museum of Zoology. Three deep pits formed by females are seen on a diagonal line across the figure. They may be distinguished by their circular shape (and straight sides) from pits formed by commensal lamellibranchs, one of which is seen to the right (oval in shape). Just above the central pit is another shallow depression which was occupied by a male.

III.

THE FAUNA ASSOCIATED WITH THE CRINOIDS OF A TROPICAL CORAL REEF: WITH ESPECIAL REFERENCE TO ITS COLOUR VARIATIONS.

BY F. A. POTTS, M. A.,

Fellow of Trinity Hall and Balfour Student of the University of Cambridge, England.

One plate and seven text-figures.

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THE FAUNA ASSOCIATED WITH THE CRINOIDS OF A TROPICAL CORAL REEF: WITH ESPECIAL REFERENCE TO ITS COLOUR VARIATIONS.

BY F. A. POTTS, M.A.

INTRODUCTION.

Although so much attention has been devoted to the phenomena of mimicry and protective resemblance displayed by land animals, in only one case has the colour resemblances of a marine animal been exhaustively studied. I refer to the classical instance of *Hippolyte varians*, illustrated by a long series of ingenious observations made by Gamble and Keeble. Briefly stated, the story is as follows: The young *Hippolyte* is free-swimming and colourless, but it becomes virtually a sedentary animal, anchoring itself to a seaweed or hydroid in the Laminarian zone, on which it finds both food and shelter. The prawn has the power of forming red, yellow, and blue pigments and by altering their relative proportions in the chromatophores it can acquire a green, brown, blue, or red ground-colour, and is thus able to adapt itself to the varied colours of the seaweeds and hydroids. The pigment may be laid down in longitudinal stripes or horizontal bars and in this way a colour scheme can be formed matching whatever seaweed the prawn shelters in. In early life a change in habitat is followed by a readjustment of the pigment altering the colour scheme, but this power is soon lost.

There are, however, a great number of cases where species of small marine animals are associated with an environment not varying, as in the case of *Hippolyte*, but definitely fixed for the species—for instance, some particular kind of sedentary animal, sponge, alcyonarian, or crinoid, as the case may be, which it frequents for shelter and commonly resembles in colour. Sometimes the first is definitely a parasite on the second, as in an example of the phenomenon often noted at Murray Island, where the bright blue starfish *Linckia lævigata*, so widely spread on the Indo-Pacific reefs, was a source of food to multitudes of tiny copepods (*Linckiomolgus cæruleus* Stebbing), whose colour exactly matches that of the host, though the pigment is of a different chemical nature.

In the majority of cases the association is of a vaguer nature, and while the associated animal gains protection it obtains its own food-supply. How numerous such cases are in tropical seas may be seen from the following passage:

> "We noticed numerous other animal partnerships, which might have been cases of commensalism but were more probably merely one-sided adaptations of one animal standing in need of protection to another animal capable of affording the required protection without any expenditure of effort. For instance, a very common branching zoophyte of this region is *Spongodes pustulosa* (or some very closely related species), a creature near akin to the 'dead men's fingers' of British seas. It looks like a small 'run to seed' cauliflower, of which the individual florets are of a bright pink colour. Hidden among its branches we found no less than four small species of crustaceans (an *Alpheus*, a *Galathea*, a *Porcellana*, and a rare little spider crab known as *Hoplophrys oatesi*), all of which, in life, are greyish white, with bright pink spots, so that they are perfectly invisible so long as they remain quiet in their living refuge. Another zoophyte that we often dredged was *Pteroeides elegans* (or a species intimately close to it), one of the seapens, of a grey colour profusely marked with little blackish rings. In its leaves three small species of crustaceans are accustomed to hide, all of which are coloured and spotted exactly like the living citadel in which they dwell. I have already mentioned the sea-lily (*Actinometra*), striped in alternate bands of yellow and purple, on whose fronds similarly striped crustaceans live without fear of detection; here we found the same sea-lily giving secure shelter to sea-worms, banded yellow and purple like itself."—(*A Naturalist in Indian Seas.* A. Alcock, London, p. 112, 1902.)

The association last mentioned in this passage, that between stalkless crinoids and a multitude of smaller invertebrates, forms the subject of this paper. To those who only know the species of *Antedon* found in our own British waters, the wealth of numbers and the riot of colour in the crinoid fauna of a tropical coral reef is a remarkable revelation. In October 1913, during my visit to Murray Island, I was able to observe this fauna under the best conditions. The commonest species there is the form *Comanthus annulatum* (Bell), remarkable for its extraordinary range of colour variation from very light-coloured individuals (in which white, light green, yellow, and grey mingled in the colour scheme) to others which are entirely dark green or black. In the shelter of its arms live commensal forms belonging to many groups of marine invertebrates, and generally speaking they possess a type of colouration which makes them inconspicuous upon the host and so varies with the colour of the host. The fact that such a relation exists between crinoids and such animals as alpheids, galatheids, and worms has been pointed out by Dana, Haswell, and Alcock, but I think the circumstances warrant the publication of a more minute though still very incomplete study of this curious phenomenon.

List of animals commensal with crinoids on the reefs of Murray Island and off Mabuiag, Torres Straits, Australia.

[Other forms described as commensals of crinoids in other areas are included in brackets. Only those forms which show colour resemblance to the host are included.]

CRUSTACEA	Decapoda Macrura Alpheidæ.	Synalpheus comatularum Haswell, S. brucei sp. n. (S. stimpsonii var. maldivensis, Indian Ocean. S. carinatus var. binongeensis, East Indies.)
	Pontoniidæ	Periclimenes commensalis Borradaile. P. pottsi Borradaile. [P. cornutus, ceratophthœlmus, brocketti, Indian Ocean.] [Pontoniopsis comanthi Borradaile.]
	Decapoda Anomura.	Galathea elegans Adam and White (G. deflexipons and longirostris are probably synonyms of this species). G. inflata sp. n. G. minuta sp. n.
	Isopoda	Cirolana lineata sp. n.
	Amphipoda	Cyclotelson gen. n. purpureum sp. n.
ECHINODERMATA.	Ophiuroidea	Amphiuridæ. Ophiactis sp.? Ophiotrichidæ. Ophiomaza cacaotica Lyman. Ophiomaza cacaotica var. picta Koehler. [Ophiophthirius actinometræ Döderlein, Torres Straits; Thursday Island. Ophioœthiops unicolor Brock, Amboina. Ophiosphæra insignis Brock, Amboina.
ANNELIDA	Polychæta	Polynoë minuta Potts var. comanthi var. n. [P. crinoidicola Potts, Indian Ocean.]
	Myzostomida.	
MOLLUSCA	Gasteropoda.	

DECAPODA MACRURA.

ALPHEIDÆ.

The species of alpheids commensal with crinoids in Torres Straits are two in number:

Synalpheus brucei sp. n. from *Comanthus annulatum* and *Comatula purpurea* on the reef at Murray Island.

S. comatularum Haswell from *Comanthus annulatum* in shallow water from localities in Torres Straits (Albany Passage, Cape York, and north of Mabuiag).

Coutière has divided the species of this huge genus *Synalpheus* into several groups, each consisting of nearly allied forms. In the *Comatularum* group those species are included which fall in the following diagnosis:

"Supraorbital spines insignificant compared to the rostrum; antennules shorter than the antennæ; spines of the basicerite almost equal, the external always smaller than the stylocerite; external maxillipeds oral, feebly spinous distally; first segment of the carpus of the second pair of feet very long, following feet cylindrical; ventral hook of the dactyl obsolete; telson with an oval median lobe."

Coutière goes on to remark that his group is—

> "differentiated from the other groups by some marked characters, which are almost all characters found in the Hippolytidæ and therefore suggest a less strong resemblance to the Reptantia; as frequently happens, there are added to these primitive characters (others) which show on the contrary, an adaptation carried very far; for instance, the strongly curved hooks and the movable finger of the small chela surpassing the fixed finger; these characters are especially marked in *S. comatularum* and are explained by its commensalism with the comatulid, being implements of attachment for the *Synalpheus*."

Both the species which I have collected belong to this group. Moreover, two other forms which are included by Coutière are distinctly stated in the original descriptions as occurring on crinoids. These are: *Synalpheus stimpsonii* var. *maldivensis*, and *Synalpheus carinatus* var. *binongeensis* (from Comatula).

Thus, 4 out of the 12 species and subspecies in the group possess this habit. As, for the most part, the different forms are only known from very few specimens, and notes on the habits or even colouration of the living animal are hardly ever given, I think it highly likely that extension of our knowledge will show that the whole group is characterized by commensalism with crinoids and possibly also by the striking colouration, so different from that of other alpheids, which are found in *S. brucei* and *S. comatularum*.

Synalpheus brucei sp. n. (Plate 1, Fig. 2.)

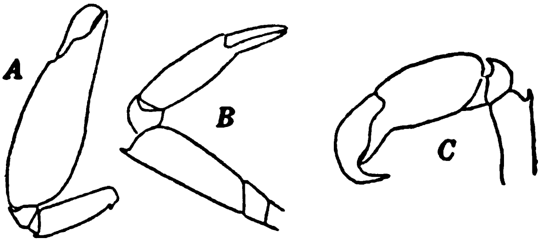

Fig. 1.—Chelæ of *Synalpheus*.
S. brucei: A, large chela, × 4; *B*, small chela, × 8.
S. comatularum: C, small chela, × 8.

A Synalpheus of medium size, commensal on crinoids. Body rather slender, colouration variable, with longitudinal bands of red or purple pigment. Rostrum very long, about one-third the length of carapace, reaching to the end of second antennular article, slender and acute, continued backwards for a short distance beyond the level of the eyes as a low carina. Supraorbital spines acute, about one-third the length of the rostrum. Antennæ (2) very long and slender; the basal joint hardly so long as the spine of the scaphocerite. Antennæ (1) very much shorter than antennæ; stylocerite only reaches to end of proximal article; proximal article much longer than other two; spines of basicerite almost equal, external does not extend further forward than supraorbital spine. Incisor process of mandible tends to end broadly, with several teeth. Large chela with rather inflated propodite, carpopodite with prominent spine on outer border. Meropodite with two smaller spines. Small chela with dactylopodite not stretching beyond end of thumb, meropodite with prominent spine on outer border. First segment of carpus of second pair of feet much longer than the four succeeding segments together. Third and fourth feet armed with sharp spine on inferior margin of meropodite; dactylopodite with distinct ventral spike measuring about one-quarter the length of joint. Telson with anterior pair of spinules, rather slender, situated just behind halfway line; median lobe oval.

Locality: Murray Islands, Torres Straits.

Measurements: In seven females measured from the tip of the rostrum to the end of the telson the length varied from 1.9 to 2.8 cm. The eggs measured 1 mm. in length; with the growth of the embryo the envelope stretches and the egg becomes twice as long. They are always light green in colour.

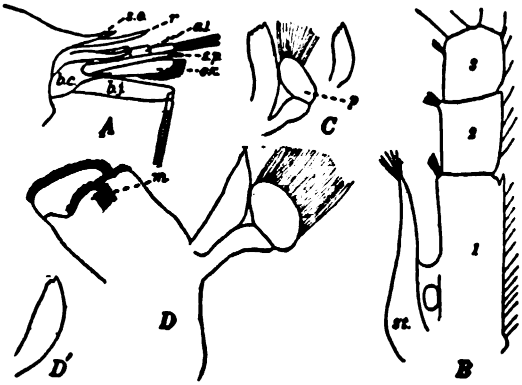

FIG. 2.—*Synalpheus brucei*: *A*. Lateral view of head showing antennæ and rostrum. *b.c.*, basicerite; *b.j.*, basal joint; *ex*, exopodite (scaphocerite); *s.p.*, spine of antenna 2; *a. 1*, antenna 1; *r*, rostrum; *s.o.*, supra-orbital spine. × 15.
B. Basal portion of antenna 1. *st.*, stylocerite; *1*, *2*, *3*, articles of protopodite. × 15.
C. Incisor process of mandibles in two individuals, one showing also palp (*p*). × 15.
S. comatularum: *D*. Mandible. Inset (*D′*) incisor process of another individual. × 15.

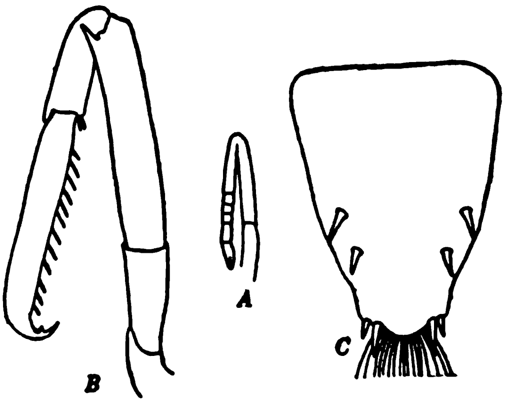

FIG. 3.—*Synalpheus brucei*: *A*, second pair of thoracic feet; *B*, third pair of feet, × 15; *C*, telson, × 15.

In these text-figures the corresponding structures of both *S. brucei* and *S. comatularum* are given for comparison in a few cases, as, for instance, the incisor process of the mandible, which, though variable in the number of teeth in both species (for this reason two examples of each are drawn to show the range) has a larger number in *S. brucei*.

RELATIONS OF COMMENSAL AND HOST.

Comanthus annulatum, with which *Synalpheus brucei* is usually associated, is very variable in colour. Some indication of this diversity is to be found in Dr. H. L. Clark's account of the Comatulids of Torres Straits. It will be sufficient here to say that the colouration varies from a light green mingled with yellow and white to the darkest green or even black. The commensal alpheid is generally black to brownish purple in ground-colour, but the pigmented dorsum is traversed by longitudinal stripes which are free from pigment. Of these one runs down the middle line from head to tail, there are either two or three on each side of the carapace, and two on the upper surface of the chela. In addition, each abdominal pleuron is traversed by a short, oblique pigment-free stripe, which may by the encroachment of the pigment become a spot. The relative extent of pigmented and non-pigmented areas is exceedingly variable and corresponds roughly to the depth of colouration of the host which the alpheid inhabits. Individuals which lodge upon a light-green coloured crinoid have only thin red or purple lines of pigment, the rest being unpigmented; in those which are associated with a dark green or black host the pigment may be spread over the whole of the dorsum.

In the vast majority of cases a pair, male and female, of alpheids is found on each comatulid. In a few cases there appeared to be only a single lodger, but then its small size seemed to show that it was too young to have acquired a mate. In most cases the pair are similarly coloured; rarely, however, there is a difference, and I will mention one case in which one member was marked with very definite and fairly wide stripes of dark pigment, while the other was uniformly covered by red pigment.

There are two factors in colour variation. The one is the character of the pigment, which ranges from a clear red to a purple so deep as to appear black. The second depends on the area of the body covered by the pigment. The former factor seems to depend very largely on the species of the host. *Synalpheus brucei* is found (though more rarely) on a second host, *Comatula purpurea*, in which reddish pigment predominates, and here the crustacean was sometimes observed to show a red pigment which covers the whole body and thus matches the host. But sometimes purple and white striped individuals are found on *Comatula purpurea*, thus transgressing the apparent needs of the species.

Among the commensals of *C. annulatum*, too, the pigment may be red or red brown. But this is only so in the cases where the coloured stripes are narrow. Where they are broader the pigment is invariably darker. The chief variations of colour, then, may be tabulated as follows:

Uniformly red-brown........................	In *C. purpurea.*
With narrow red stripes.....................	In light-green varieties of *C. annulatum.*
With purple stripes or uniform dark colouration..	In dark-green varieties of *C. annulatum.*

The purple pigment would seem to be either something additional or a more complex product of the red pigment. In alpheids which were preserved in formalin and glycerin to keep the original colour as far as possible, the purple was speedily lost, leaving such a red as occurs in the lighter-coloured forms.

Synalpheus brucei thus exhibits a marked protective resemblance to its host. Against the very light-coloured crinoids the almost colourless alpheid is quite inconspicuous. The striped specimens are found upon crinoids where bars of light and dark pigments alternate, and so they too are not easily seen. And lastly, when the dark pigment is uniformly spread over the body of the crinoid this is also the case with the alpheid.

But though this is often true, there are many cases where the resemblance is by no means close and the alpheid is rather conspicuous. I am inclined to explain these cases by supposing the alpheids to have migrated from some other crinoid at a comparatively recent period. So thickly do the crinoids lie in the crevices of the reef, all conceivable colour-varieties being herded together without distinction, that it is more than likely that an interchange of commensals should occasionally take place; for *Synalpheus*, though tending to become a truly sedentary animal, is at times very active and an excellent swimmer. I should also like to suggest that the conditions of commensalism do not allow natural selection to come into play to any marked extent. The commensals are for the most part inclosed by the arms of the crinoid as in a living cage. When the water is calm these arms are relaxed and extended, but on the approach of an intruder they curl up and so protect the soft central disc. It is hardly to be supposed that even a rapacious fish would take a mouthful of these hard and unsatisfying arms for the sake of the shrimp which lies amongst them. In no case at least which we saw were the arms of crinoids mutilated.

Gamble and Keeble have shown that in the prawn *Hippolyte* the young larva is at first a colourless creature living at the surface of the sea, and when this is carried inshore it attaches itself to the first seaweed it meets. The skin is in such a sensitive condition that within a week a complete resemblance in colour is brought about, whether the seaweed background be red, green, or brown. It seems that the resemblance in colouring of *Synalpheus* to its host is a similar phenomenon. But it is less perfect because natural selection has not been brought into play to the same extent (if at all) as in *Hippolyte*, whose seaweeds offer it a holdfast but not a complete refuge such as the crinoid affords.

Generally, both members of a pair are similarly coloured. This is a phenomenon which may be explained in two different ways. Either mating takes place early, before the pigment pattern has been finally determined, and the same causes act equally on both, producing a similar pattern, or else there is assortative mating. Possibly the truth lies in a combination of both explanations. If so, the exceptions where mates are dissimilarly coloured are due to the breaking down of the rule of assortative mating or the existence of individuals which are not able to assimilate themselves to their background.

With regard to the habits of *S. brucei*, it is usual to find the male and female lying side by side on the surface of the disc, but when disturbed they take refuge between the pinnules or on the aboral surface of the arms. They thus move about quite freely, but they can guard against forcible detachment by digging the claws of the thoracic legs into the soft flesh of the disc or by clasping the pinnules or arms of the crinoid. The chelæ are less effective for maintaining a hold than the thoracic legs, but it is to be noticed that these can not be said to be specially modified for this purpose. They are provided with two sharp claws, but this provision is also made in cases where the alpheid has no such commensal habits.

When removed from the crinoids they swim about very rapidly, but return as soon as possible to the shelter of the host, and cling to it as before. They exhibit reactions to light and touch in a very marked manner. Alpheids placed in a glass vessel always cluster together on the side of the vessel opposite from the light. Besides being negatively heliotropic, they are strongly thigmotropic, for when the finger is introduced into the water it is instantly embraced by the thoracic legs of the alpheid. In the absence of any foreign object, the alpheids embrace one another, so that a number left together in a vessel soon look like a mass of swarming bees.

There seems to be a limited faculty of colour change. One individual with wide stripes of pigment became lighter toward night, darker again at day. Unfortunately I did not make any extended observations on this point.

Synalpheus comatularum (Haswell). (Plate 1, Fig. 1.)

Alpheus comatularum, HASWELL, Proc. Linn. Soc., N. S. Wales, vol. 6; Catalogue of the Australian Stalk and Sessile Eyed Crustacea, Australian Mus., pp. 189–90.

This species was dredged in a few fathoms of water in Albany Passage, near Cape York, during the cruise of H. M. S. *Alert*. "They were invariably found clinging to the arms of a species of comatulid to which their markings gave them a general resemblance." It was also obtained during the voyage of the *Challenger*, in neighbouring waters and off Ceylon, by Professor Herdman.

We did not find this form at Murray Island, but during a visit to the western Islands of Torres Straits, in the early days of November, I obtained it in 3 to 5 fathoms off the great reefs lying north of Mabuiag Island. With the greatest kindness, Mr. Walker, managing director of the Papuan Industries Co., Ltd., put the company's schooner *Dogai* at my disposal and, with three divers from Badu in addition to the ordinary crew, I spent a couple of days on the Mabuiag pearling grounds. For an hour or more at slack tide the most wonderful crinoids were to be collected by diving. The species so common at Murray Island (*Comanthus annulatum*) was the dominant form here, but represented by individuals even larger and more splendid in colour than those inhabiting the reefs of the Murray Islands.

S. comatularum is markedly larger than *S. brucei* and is stouter in general appearance. But the resemblance in colouration and habits is so close as to suggest specific identity until the peculiar form of the little chela is noticed. It is this feature which distinguishes the type species from all the others included in the *comatularum* group. The thumb is much longer than its unmovable fellow and forms a strong recurved hook, by means of which, Haswell remarked, it clung to the arm of the crinoid. The individuals taken on the *Dogai* were generally seated in pairs on the disc, like *S. brucei*, but when slightly disturbed they immediately dug the hook of this chela into the flesh of the disc, from which it was only dislodged with difficulty; or if the alpheid had left the surface of the disc, the chela was serviceable for clasping the arm of its host. But this instrument is only used for temporary attachment, nor is it usually embedded in the host when the animal is at rest.

The wonderful similarity in colouring between the two species of *Synalpheus* is noticed above. There is, however, one marked difference; that is, the entrace of a white or yellow pigment into the colour scheme of *S. comatularum*. A typical example of a light-coloured crinoid and its commensal may be briefly described here.

The crinoid (*C. annulatum*) had a yellow-green disc, the arms were black with white tips, sometimes with a dash of rusty-red pigment, and the pinnules white, sometimes grey at the side. The underside of the arms was yellow-green and the cirri were white. Both the commensals were light coloured and harmonized to a considerable extent with the host. The female had five prominent lines of white pigment on the thorax alternating with brown lines; in the abdomen there was a median white line with a brown line on each side, most of the median space being colourless and a non-pigmented eye being found on each pleuron. The male showed 6 lines of brownish-purple pigment on the thorax, all else being colourless, save for some dashes of white pigment. In this case the two partners differed slightly; the female showed well-developed white pigment and the other pigment was brown; in the male white pigment was almost absent and the pattern was formed by a purple-brown darker than in the female.

PONTONIIDÆ.

Three prawns of this family, all new to science, were found to be characteristic members of the crinoid fauna. These are: *Pontoniopsis comanthi*, *Periclimenes pottsi* and *P. commensalis*. They have all been examined by Mr. L. A. Borradaile and full diagnoses have appeared in his recent revision of the family. I will confine myself here to giving the details of their colouration and habits which were noted.

Pontoniopsis comanthi Borradaile.

This was found only at Mabuiag on the light-coloured varieties of *Comanthus annulatum* in which a great deal of green pigment had developed. In general this small crustacean (it is about 8 mm. long) exhibits a striking correspondence with its host. Alternate longitudinal stripes of bright green and black or dark brown occur on the dorsum, and these match with the crinoid cirri, in which green and yellow alternate with dark green or black. There also occurs another variety, in which the green pigment is replaced by yellow and the darker pigment by red or brown. In the specimen figured (pl. 1, fig. 3), which is typical of the species, there were three yellow stripes alternating with two brown of equal breadth. The chela was yellow with a brown line. In this case, however, the commensal, living on a crinoid in which green predominated, was very conspicuous, and I suppose it to have developed its pigment in association with another crinoid of different colour type.

Periclimenes pottsi Borradaile.

This shrimp is comparatively common on the crinoids from the Murray Island reef, but only one or two specimens were obtained at Mabuiag. It is a very transparent creature, and though the general colouration, a beautiful purple, harmonises with the host, there is no distinct arrangement in longitudinal stripes. The low power of the microscopes shows that there is a blue pigment contained in very numerous small cells which are regularly disposed over the body. Also evenly distributed, but much fewer in number, are cells containing red pigment. These may be spherical or branching. The gut is coloured red. The general effect is thus purple.

Periclimenes commensalis Borradaile.

I did not, amongst the living specimens, distinguish this species from *P. pottsi*, so probably what has been said about the latter species also applies to the former. It may be noticed that these are not the only species of the genus *Periclimenes* to be found in association with crinoids. Others are *P. cornutus*, *ceratophthalmus*, and *brocketti*, all found on crinoids from the Maldives, as noted by Professor J. Stanley Gardiner.

Information about the surroundings of the animals so seldom accompanies general collections that I fully expect a similar connection to exist in the case of many other species of this enormous genus.

DECAPODA ANOMURA.

GALATHEIDÆ.

There are at least three species of galatheids commensal with crinoids in Torres Straits. These are: *Galathea longirostris* (=*G. elegans*), *G. inflata* sp. n., *G. minuta* sp. n. These are all small forms from 6 to 15 mm. in carapace length and are dark coloured with longitudinal, pigment-free bands, a colour scheme corresponding almost exactly to that of the alpheids. They are not by any means found so commonly as is *Synalpheus*, though *G. longirostris* is not infrequent. My observations do not lead me to suppose that the galatheids occur in pairs on each host, but the absence of evidence on this point may be due to the fact that they are inclined to leave the host whenever disturbed. There is no special modification for clinging to the crinoid other than the spines on the dactyli of the thoracic legs, but the animals are thigmotropic and swim back immediately to the host when they have been detached.

Galathea elegans Adam and White. (Plate 1, Fig. 5.)

G. elegans, Adam and White, Voyage of the *Samarang*.
G. longirostris, Dana.
G. deflexipous, Haswell, Proc. Linn. Soc. New South Wales, vol. vi; Miers, Zool. Coll. H. M. S. *Alert*.
G. longirostris, Southwell, Anomura, Ceylon Pearl Oyster Rep. Roy. Soc., part V, p. 220, 1906.

In earlier literature there are only three records of the occurrence of galatheids on crinoids. The first is that of Dana, who originally described *G. longirostris* from a crinoid dredged at Fiji; the second is that of Haswell, who founded a new species *G. deflexipous*, associated with *Synalpheus comatularum* on an unidentified crinoid. The third likewise concerns *G. longirostris*, which is mentioned by Southwell as obtained near Ceylon, clinging to *Antedon bella*.

G. elegans Adam and White, *G. longirostris* Dana, and *G. deflexipous* are all very closely related. They all possess a long rostrum with from 5 to 10 small lateral denticles, a very typical dorsal ornamentation, and have a similar colour scheme, with longitudinal stripes of pigment on the dorsum. The first-named species has not been noted as occurring on crinoids, but this may be the fault of the collectors. Balss, in describing a specimen from Japan, which he assigns with some doubt to *G. elegans*, says with regard to its occurrence: "Wahescheinlich an Comatuliden, wie es Haswell von der nahe verwandten *G. deflexipous* und Southwell von *G. longirostris* Dana angeben. Darauf weist die bunte Färbung hin, die wohl als eine mimetische su deutenist." Probably the whole group of related species are crinoid dwellers. If not, it will be strange that so marked a pattern should occur on a free-living galatheid, when that is a character so definitely associated with crinoid commensalism, both here and in other groups.

The three species are principally defined with regard to the characters of the rostrum; thus:

G. elegans:	*G. longirostris:*	*G. deflexipous:*
Rostrum more than half the length of the rest of the carapace, "with 7 small denticulations on each side" (Haswell). But Balss gives the latter number as 9. But most important of all, the original figure only shows 5 or 6.	Rostrum fully as long as half the carapace "minutely 5–6 serrulate."	Differs from *elegans* only in the fact that the rostrum is entirely deflexed.

With regard to the third species Miers says:

> "In more than one of the specimens in the Museum collection the rostrum is slightly deflexed, and I think that *G. deflexipous* Haswell, from Albany Passage, should be regarded merely as a marked variety of *G. elegans*."

In my own specimens the number of denticulations on each side is from 6 to 7; in one individual there were 6 on one side, 7 on the other.

There are also a number of cases in which the rostrum is deflexed. From the comparison here made and the facts stated I think there is little doubt that we are dealing with one very variable species.

I have compared my collection with the full description given by Balss of his specimen (the fullest description given of *G. elegans*) and find the following discrepancies:

(1) In the third maxilliped the merus is armed with three prominent spines on the internal border in the Japanese form, in mine with only two; Henderson and Ortmann both describe *G. elegans* with two spines in this position.

(2) In the ambulatory limbs the merus has a spinose upper angle according to Balss, but is smooth in the Torres Straits forms; the denticulation of the dactylus is weak in the former, but in the latter there is a powerful end claw, succeeded by prominent teeth only gradually decreasing in size.

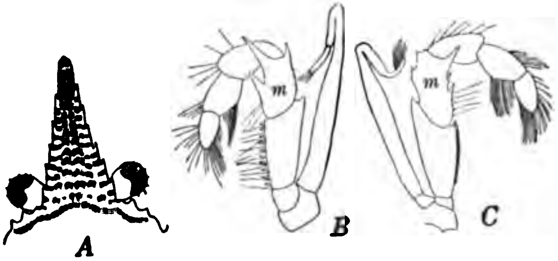

FIG. 4.—*Galathea.*

A. *G. elegans*, Torres Straits, rostrum showing lateral teeth and arrangement of hairs. × 8.
B. *G. minuta*, third maxilliped, showing spines on merus (*m*). × 18.
C. *G. inflata*, third maxilliped. × 4.

But in a variable species we might expect to find such differences. The Japanese form described by Balss is clearly a rather extreme member of the variable series, as shown by the fact that it has the highest number of denticulations on the rostrum recorded. The agreements between Balss's description and my specimens outweigh the differences.

In conclusion, I give the following diagnosis, to embrace all the forms here discussed:

G. elegans: Rostrum rather more than half the length of the remainder of the carapace with from 5 to 9 small denticulations on each side; width about half the length; sometimes deflexed; carapace somewhat pear-shaped; about a dozen indentations on each side; surface traversed by many narrow horizontal furrows, from which spring thick lines of short fine hairs, though these may be absent or nearly so. The rostrum is covered with hairs rather longer than those on the carapace, arranged in distinct crescents posteriorly. Dorsum and limbs covered with dark pigment, but there are generally pigment-free longitudinal bands of variable width. Chelæ long and slender, cylindrical in section, thicker in the male than the female, varying in length in the latter.

Often, if not always, commensal with crinoids.

Measurements of Torres Straits specimens (a female with eggs): Length of carapace 11 mm.; maximum breadth 6 mm.; length of rostrum 4.5 mm.; length of chela 15 mm. (of propodite 7 mm., carpopodite 2.5 mm., meropodite 5 mm.)

Another small male: Length of carapace 6 mm.; breadth 3.5 mm.; length of rostrum 2.5 mm.; of chela, 9.5 mm. (propodite 4, carpopodite 1.5, meropodite 4).

So far as I can find, there is no description of *Galathea elegans* White, but only the figure. From this, however, I think it is possible to assert its community with the other forms under discussion. Balss queries his Japanese individual because its chelæ are more slender and longer than those in White's drawing and because the width of the colour bands is different. In my Torres Straits collection, as I have repeatedly observed, the width of the bands is a variable feature, so the latter point need not trouble us. The discrepancy of the chelæ is likewise to be explained by variation and possibly, to a certain extent, by the draughtsman's error.

I have taken the opportunity of comparing my series with a specimen obtained by Dr. Willey in New Britain and identified by Mr. L. A. Borradaile as *G. elegans*. This certainly differs distinctly from the commensal of *Comanthus* in the following particulars: It has a broader but rather shorter rostrum with more (9) lateral denticles. The eyes are larger, the transverse furrows on the dorsum not so well developed, hairs are almost absent on the greater part of the carapace but present on the rostrum. Here they are arranged in just the manner characteristic of the animals from the Torres Straits. This individual seems to come nearer to that described by Balss from Japan.

Galathea inflata sp. n. (Plate 1, Fig. 7.)

A small galatheid with rather broad and swollen carapace narrowing considerably anteriorly; rostrum of medium length with 3 sharp spines on each side; carapace with very few hairs, gastric region without spines, anterior transverse ridges broken up and surface covered with scales. Merus of third maxilliped with 3 spines internally, 2 externally. Merus of ambulatory limbs with about 9 spines on upper border.

Commensal with crinoids, Murray Island, Torres Straits.

With eggs, length of carapace to tip of middle spine on rostrum, 7 mm.; breadth 5 mm.; length of rostrum 2.5 mm.

The carapace is traversed by only 7 or 8 traverse grooves, but posteriorly incipient grooves make their appearance between the complete ones at the lateral extremities of the segments. The cervical groove is deep and continuous; on each side of it the traverse ridges are broken up into prominent scales. The external border of the cephalothorax has about 7 strong spines on each side.

The rostrum is broad and of medium length. The central spine is long and stout; on each side are two others, almost as well developed, and a third at the level of the eye which is shorter and weaker. The surface is covered with small scales.

The basal joint of the first antenna is provided with 3 spines, the dorsal of which is longer and stronger.

On the merus of the third maxilliped there are internally 3 spines, the middle one being the shortest; externally are 2 very blunt spines; the teeth on the inner border of the ischiopodite are small and numerous.

The chelæ are missing in this specimen. The ambulatory limbs are rather thickly beset with long coarse hairs; spines on the merus not very well developed, but spines on the carpus very prominent. Dactylopodite with strong spine after end claw, others small.

Colouration: Dark-blue pigment on carapace, with two fairly broad longitudinal pigment-free bands.

On *Comanthus annulatum* were a few very small galatheids, white in colour, with rather thin and membranous cuticle. Two which were examined in detail were females with eggs and could not have moulted very recently. In these the form of the rostrum comes very close to *G. inflata*. It is short and broad, armed with 4 spines on each side, of which the 3 anterior are prominent, almost as large as the median spine, and the fourth is much smaller. They differ from *G. inflata* mainly in the fact that the median spine is the same size as those which follow instead of being distinctly larger. The rostrum is covered by coarse hairs. The carapace is traversed by transverse grooves, but in one specimen (the larger) these are broken up at the side into rounded scales, while in the other the lines run interruptedly across. The carapace is not pear-shaped, as in *G. inflata*. In another point the two individuals differ considerably, that is, the development of the third maxilliped, which in the larger form possesses 2 spines on the inner side of the merus and some very small blunt processes on the outer border. In the smaller form (which was parasitised by a bopyrid) there is only a single spine on the inside, while the outside is smooth.

It seems possible that we are dealing with a variable species or possibly a group of species which has the rostrum character described above, while the carapace shape and to a certain extent its ornamentation varies with the size of the individual. The character of the third maxilliped is also variable, the number of spines on the merus increasing with age.

With regard to the strong development of pigment in one and its non-appearance in others, in spite of the fact that all were found on crinoids, I can make no suggestion of any importance. It may be that in a variable species some individuals are incapable of an assumption of pigment. It is not to be supposed, I think, that these unpigmented individuals had but recently taken up their residence in the crinoids, for they were mature females with eggs. However, I can not pretend to explain, on the strength of only three specimens collected, a phenomenon which is of so much biological interest.

For the present, then, I wish to recognize an "*inflata*" group, distinguished by the short, broad rostrum with 3 or 4 spines on each side (of which the last is the smallest) and the absence of spinulæ on the gastric region. They differ from *multilineata* in having a shorter rostrum and longer spines and in the far less marked sculpturing on the carapace.

Galathea minuta sp. n. (Plate 1, Fig. 6.)

A very small galatheid, with short and broad rostrum, 3 sharp spines on each side; gastric region without spines, carapace with few hairs, traversed by about 12 shallow transverse grooves; chelæ short; merus of third maxilliped with 2 strong spines internally, one externally.

From *Comanthus annulatum*, obtained in about 4 fathoms of water off Mabuiag Island, Torres Straits, Australia.

Measurements: Length of cephalothorax to tip of rostrum 4.5 mm. Length of chela 6.2 mm., of propodite 2.7 mm. Breadth of cephalothorax 3 mm. Length of carpopodite 1.0 mm., of meropodite 2.5 cm.

The carapace is of fairly uniform breadth, narrowing slightly and gradually anteriorly. Its surface is smooth, traversed by only about 12 shallow grooves, in which lie scanty rows of short hairs. There are no spines on the gastric region, but prominent spines (8 in number) exist at the end of the transverse grooves.

The rostrum is rather short and broad. The central spine is very strong and elongated and on each side of it are 3 prominent spines with their bases close together and advanced, also strong and elongated. The surface is smooth.

The basal joint of the first antenna carries 3 anteriorly directed spines; the dorsal one is long, the two ventral smaller and more slender.

The merus of the third maxilliped carries 2 large spines internally and one, rather shorter, externally followed by small spinulæ. The teeth on the internal border of the ischiopodite are comparatively few and strong.

Abdomen with two transverse lines to each segment.

Chelæ short, about half as long again as the cephalothorax, beset with long, coarse, scattered hairs and strong spines on the propodite, carpopodite, and meropodite, especially the carpopodite. Dactylopodite little more than a third of the propodite in length.

Merus of ambulatory legs beset on upper angle with about 10 spines, very small proximally, prominent distally. Dactylopodite with strong end claw and one prominent spine succeeded by minute processes.

Colouration: Alternate longitudinal stripes of white and dark blue, as shown in plate, of about equal breadth. On a light-coloured individual of *Comanthus annulatum.*

AMPHIPODA.

A tiny amphipod which occurred very often on the darker crinoids is apparently to be referred to the family *Amphilochidæ*, a new genus of which must be established for its reception.

CYCLOTELSON gen. n.

Rostrum curved, acuminate, lateral angles of head rounded. Side plate 1 not much smaller than 2, rounded, obscured by those succeeding it; 2 to 4 large and deep, 2 and 3 rounded, 4 largest, quadrangular shape (also 5) as in *Amphilochus.* Antenna 1 very short and stout, flagellum particularly so. No accessory flagellum, upper lip bilobed, lower lip with small inner lobes. Mandible with very narrow denticulate cutting edge, molar process absent, third joint of palp very long. Maxilla 1, inner plate absent, outer plate with 8 or 9 spines, the proximal much the largest and forming dentate process pointing inwards; palp very broad, 2-jointed. Maxilla 2 normal. Maxilliped inner plate elongate, palp rather long. Gnathopods 1 and 2 similar, nearly the same size, subchelate, palm not so long as in *Amphilochus*, broad, distal edge rather oblique, broadest part of palm, finger with sharp spine under apex. Peræopods 1 to 5 slender, 3 to 5 with second joint expanded. Telson comparatively broad with rounded termination. Lateral angles of last abdominal segment as long as telson itself.

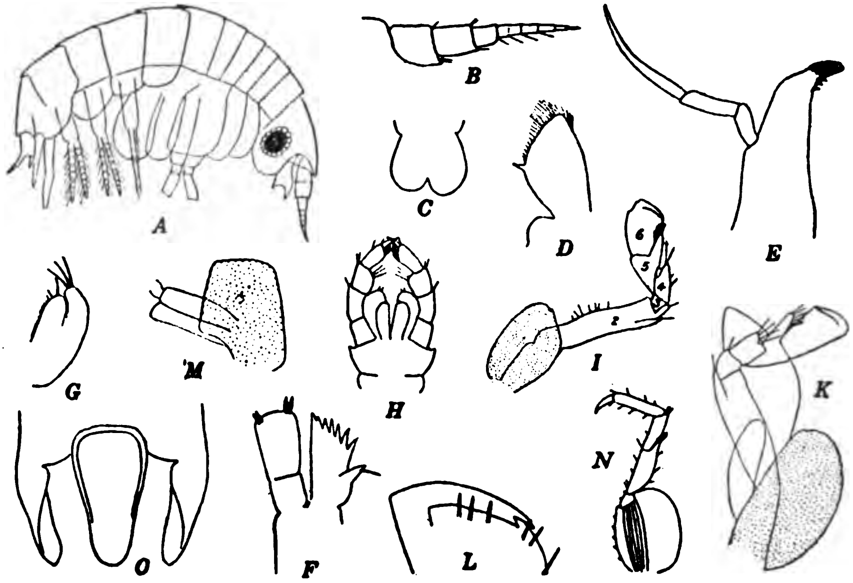

FIG. 5.—*Cyclotelson purpureum* gen. et sp. nov.

A. Whole animal, lateral view. ×17.
B. Antenna 1. ×52.
C. Upper lip. ×225.
D. Lower lip (half). ×225.
E. Mandible. ×130.
F. Maxilla 1. ×130.
G. Maxilla 2. ×130.
H. Maxilliped. ×52.
I. Gnathopod 1. ×52.
K. Gnathopod 2. ×52.
L. Gnathopod 2: finger and anterior edge of palm. ×225.
M. Side plate 4 with first joint of peræopod 2. (Lateral plate dotted.) ×30.
N. Peræopod 4. ×30.
O. Telson and lateral angles of last abdominal segment. ×130.

Cyclotelson purpureum sp. n.

Side plates vary in serration of lower and posterior margins: 1 with single serration, 2 with about 10, 3 and 4 with many. Antenna 1 six-jointed with very few sensory setæ, no appreciable difference between male and female. Antenna 2 incomplete in specimens examined, but from width of basal joints seems to be distinctly larger than 1. Outer lobe of lower lip with fringe sisetæ and an inwardly directed spine. Mandible with third joint of palp dot tinctly longer than 1 and 2 combined, no setæ on palp; three small spinules under incisor process. Gnathopods 1 and 2, sixth joint widens gradually of form a convex palm with slightly oblique anterior edge; finger stout, equal in length to front edge of palm, minute serrations behind subapical spine; fifth joint produced to about middle of the palm, process broad; second point produced slightly. Telson width more than half length, apex rather rounded.

Colour, purple on dorsum. Lives on crinoids. *Comanthus annulatum*, Murray Islands, Torres Straits.

ISOPODA.

Cirolana lineata sp. n. (Plate 1, Fig. 4.)

This species comes under the second section of the genus as divided by Hansen,* in which are included all species with the following characters:

"Lamina frontalis inermis, lata brevis, pentagona (varius fere hexagona), vix dimidio longior quam latior.

"Clypeus inermis, non cornutus, ante perspicue cum lamina frontali conjunctus.

"Antennulae pedunculo obscure triarticulato (primo visu biarticulato) flagello semper satis gracili.†

"Pedes omnes setis perpaucis vel nullis instructis."

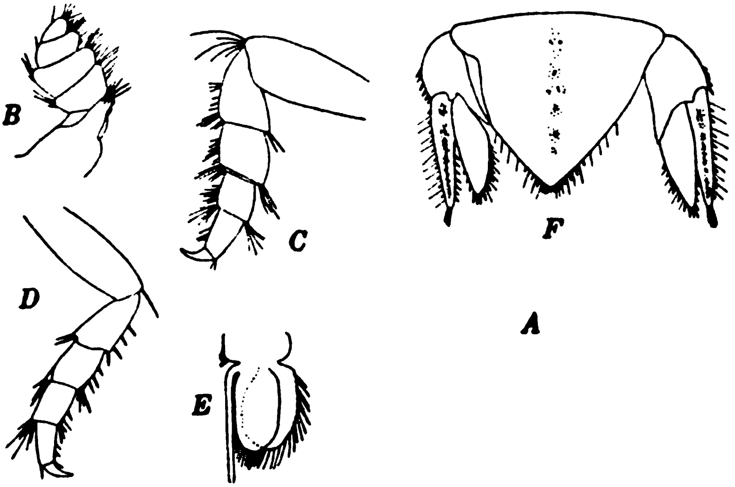

Fig. 6.—*Cirolana lineata* sp. n.

For whole animal see plate 1, fig. 4. All figures except E are of the female.

A. Antennæ and frontal lamina.‡
B. Maxilliped. ×38.
C. Sixth thoracic leg. ×18.
D. Seventh thoracic leg. ×18.
E. Second pleopod of male, showing appendix masculina. ×18.
F. Telson and uropoda. ×18.

Diagnosis: A small cirolanid, body ovate (female), rather more than twice as long as broad. Measurements, female 6 mm. in length, 2.5 mm. in breadth; male 4.7 mm. in length, 1.5 mm. in breadth. Occurs on crinoids, generally *Comanthus annulatum,* in Torres Straits. Colour white except, for branding chromatophores carrying a purple pigment and arranged in two lateral stripes and a fainter median line.

Head wider than long, anterior margin rounded. Eyes of medium size. First antenna stout, first joint of peduncle large, second a little smaller, and

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*Hansen: Cirolanidæ et familiæ nonnullæ propinquæ Musei Hauniensis. Kjobenhavn. 1890. See p. 336.

†But I take exception to the definition of the peduncle as always so obscurely triarticulate; and the condition of the peduncle in my species seems to resemble that in *C. parva* established by Hansen, which from the figure is clearly triarticulate.

‡The duties of the author as an officer in the British Army, prevented his attention to this paper as it was going through the press, and figure A was unobtainable.

third much smaller; flagellum composed of about 8 joints. Second antenna more slender than the first but not very much longer; in the peduncle the first two joints are very small and equal; the third is as long as the first two together, the fourth longer still, and the fifth about as long as the third; the flagellum is composed of 7 joints and extends very little beyond the lateral margin of the first segment. The frontal lamina is pentagonal, scarcely twice as long as broad.

Maxilliped second joint much longer than those succeeding, which are very broad. First thoracic segment nearly twice as long as the second; the posterior six segments vary slightly among themselves. Appendages robust, all joints broad, with few setæ.

First segment of abdomen quite hidden below last thoracic. Telson forms an equilateral triangle, ending in a sharp apex with 16 to 18 spines on the posterior margin, surface smooth. Inner ramus of uropod extends a little further than the telson, is narrow and ends in a sharp apex; both margins are furnished with spines; outer ramus about the same length, but still narrower; peduncle not produced far posteriorly on inside.

Appendix masculina slender, much longer than inner ramus of second uropod, apex rounded.

This species is very distinct. It is separated from all others by the insignificant length of the second antenna, and also, so far as I can find from the published descriptions, by the character of the colour markings. The shape of the telson and especially of the uropods is also very distinctive.

All the members of the Cirolaninæ to which this species belongs are predatory and swim about very actively. *Cirolana lineata* is far from being as sedentary as *Synalpheus*, which, while very energetic at times, rests for long periods on the disc of the crinoid. While the isopod may make busy excursions onto the surface of *Comanthus*, it is often to be seen diving into the gut of the host, where it apparently spends a large part of its time. It does not feed, so far as I know, on the tissues of the crinoid itself, but only on the food it finds in the stomach.

It must be this or a very closely related form which Haswell refers to as collected from a crinoid in Torres Straits associated with *Synalpheus comatularum* and *Galathea deflexipous*, but no identification of his isopod seems to have been made.

This case of commensalism is interesting because of the faint but significant response to the colour stimuli of the crinoid. In nearly all the species of this genus, where the colouration is noted at all, the chromatophores appear to be distributed over the surface so as to form a series of evenly spaced dots or dashes of pigment. The concentration of these into lines and the development of a purplish pigment seem to be the first effects of the commensalism. The insignificant quantitative development of the pigment is probably associated with the very active life of the isopod and its frequent immersion in the gut of the host, rather than to any incapacity of the isopod to assume the colours of the environment.

ECHINODERMS.

The only echinoderms which were found associated with the crinoids were ophiurans, and of these only one genus (*Ophiomaza*) is characteristically commensal. A small species of *Ophiactis*, which seems to be as yet undescribed, and a young *Ophiocoma*, too small for accurate determination, were found on *Comanthus annulatum*, but it was not possible to determine whether this association was anything more than accidental. But of *Ophiomaza* a sufficient number of specimens was found to show that that genus is normally commensal. All the individuals taken were on comatulids; none were seen elsewhere. On *Comanthus annulatum* were found specimens of *Ophiomaza cacaotica*, uniformly black (or very deep purple or brown); *O. cacaotica* var. *picta*, prettily marked with black and white; and *O. obscura*, brown, handsomely marked with dull yellow. In all these cases, a certain amount of correlation between the colour of the ophiuran and the colour of the host was obvious. But on a bright red *Comatula purpurea* was found a small black specimen of *O. cacaotica*, and of course the colour contrast was very striking. However, *Ophiomaza* was much too rare to permit any reliable deductions to be drawn concerning the influence of commensalism on the colouration.

POLYCHÆTA.

Polynoë minuta Potts var. oculata var. n.

This polychæte, which I found rather frequently on the darker varieties of *Comanthus annulatum*, undoubtedly comes nearest to *Polynoë? minuta*, which I described in 1910 from specimens collected by Professor J. Stanley Gardiner in the Maldives.* It was not stated that this form occurred upon crinoids, although the labels of the various specimens of *P. crinoidicola*, in the same collection, gave quite definite information

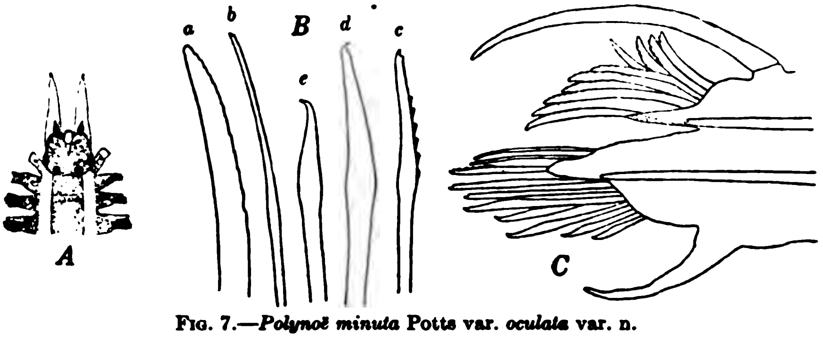

FIG. 7.—*Polynoë minuta* Potts var. *oculata* var. n.

A. Head and anterior part of dorsum to show colour pattern; median tentacle, tentacular cirri, and dorsal cirri all wanting. ×8.

B. Setæ. *a*, dorsal; *b–e*, ventral.

C. Parapodium of sixth segment. ×65.

References in text: *A*, *B*, *C*, ×163; *D*, *E*, ×280.

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*Trans. Linn. Soc., London, vol. XIII, pt. 2, Polychæta of the Indian Ocean; pt. II, The Palmyridæ, Aphroditidæ, Acœtidæ, and Sigalionidæ. See p. 337.

of such an association in this latter case. As we do not know whether the original species is a commensal of crinoids, and in view of certain morphological discrepancies, I describe the Torres Straits form as a new variety.

The two cotypes of *P. minuta* were incomplete individuals and on this account the generic ascription was queried. In the series under consideration there are three complete individuals, each having 15 pairs of elytra. There is no reason why this species should not be definitely assigned to the genus *Polynoë*, though there is good reason for undertaking a revision of this and kindred genera.

The characters which separate the Torres Straits form from the original species are as follows:

(1) The head is provided with two pairs of very distinct eyes, the one placed laterally near the posterior angle, the other on the posterior border. The head is covered with dark pigment, but there is a pigment-free ring round the posterior eyes (the depression separating the two lobes of the head is free also). In the Maldivian individuals there were no signs of eyes.

(2) The lateral tentacles have a much swollen base—in the type species they are thin throughout. The lateral anterior angles are rounded instead of slightly pointed. The palps are rather longer in proportion to the size of the animal.

There are a number of additional points, some of which could not be mentioned in the original account, which are treated below:

Colouration: The dorsum, with the exception of 2 longitudinal pigment-free bands, is covered by dark brown pigment, not soluble in 70 per cent alcohol. The markings are hidden by the elytra, which are uniformly pigmented.

Shape: In smaller specimens tapering rather abruptly, in a larger one of uniform breadth up to end.

Number of elytra: Fifteen. They cover almost the entire dorsum.

Setæ of neuropodium: These fall into the following categories: (1) Very long and slender, long drawn-out head slightly enlarged, ending in a blunt apex with a projecting tooth of almost equal size underneath (type B). (2) Thicker, head more pronounced, sharp incurved apex with prominent tooth underneath; one or two of the dorsalmost often have prominent spines on the convex surface of the head (C). Ventrally, however, spines are never present (D) and they pass into (3) a still stouter type with shorter head, apex still more incurved, tooth not so prominent (and in the ventralmost altogether absent (E)).

This succession of setæ is almost identical with that in *P. minuta*, as I find on comparison with the type specimens, which I did not describe with sufficient fulness in 1910. Setæ of type 1 occur there, though they were not mentioned or described; the other types were given, and the only difference is the absence of setæ with a very definite row of spines in *P. minuta*.

Measurements: Those of three complete individuals are given:

Specimen.	Length.	Breadth, including parapodia.	No. of segments.
	mm.	*mm.*	
A........	10	2	50
B........	8	1.75	39
C........	6	1.5	33

In conclusion, this species is quite distinct from, though related to, *Polynoë crinoidicola,* a species found on various unnamed crinoids in the Maldives by Professor Gardiner and described by me in 1910. The differences lie in the shape of the head and the tentacles and in the neuropodial setæ, but the general facies and the character of the elytra and the shape of the parapodia and of the dorsal setæ are similar. The specimens of *crinoidicola* are spoken of in one case as coming from a black crinoid and being themselves black when alive, though the pigment has dissolved out in alcohol. In other cases where the colour of the live animal and the host were not stated, the specimens were dark red. It seems certain, then, that the same type of colour resemblance occurs in the two species. In Torres Straits, too, I found the commensals always of a dark, almost black appearance and frequenting dark-coloured crinoids. They must, I think, be absent or rare on the lighter coloured hosts.

The only other reference of which I have knowledge to commensalism between a polychæte (?) and a crinoid is in Alcock's "A Naturalist in Indian Seas," p. 113, where he mentions a "sea-lily (*Actinometra*) striped in alternate bands of yellow and purple, on whose fronds similarly striped crustaceans live without fear of detection;" which in some places also gives "secure shelter to seaworms, banded yellow and purple like itself." This indicates a much wider range of pigmentation than in the present case. The banding is probably longitudinal, as in all other cases of commensalism.

THE COLOURATION OF THE MYZOSTOMIDS AND ITS RELATION TO THAT OF THEIR HOSTS.

From time to time remarks have been made on this subject. Semper* relates that he found his *M. tuberculosum,* which is spotted with red and yellow, only on variegated Comatulas, while the uniformly coloured *M. cirriferum* is found only on the red Comatulas, which it matches in colour. Von Graff,† however, remarks that though *M. glabrum* has a number of pronounced colour varieties, and the host *Comatula europæa* s. *mediterranea* varies within the same limits and almost with the identical shades of colour, yet his experience leads him to deny that any such definite mimicry relation exists between crinoid and myzostomid. A special investigation of over 200 comatulids showed that blackish, yellow and white myzostomids were just as frequently to be found on red Comatulids as blood-red myzostomids on variegated comatulids, and that the two kinds specially mentioned by Semper are uniformly distributed on the different colour varieties of the crinoid.

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*Semper, Zur Anatomie und Entwickelungsgeschichte der Gattung Myzostoma. Zeits. f. wiss. Zool. Bd. ix, pp. 48–65, 1858.

†von Graff, Das Genus Myzostoma. p. 77, Leipzig, 1877.

Von Graff quotes, however, a passage from a letter written by von Willemoes Suhm,* showing that myzostomids may correspond perfectly with their host in colour pattern. The case mentioned is that of *Myzostoma horologium* v. Graff on crinoids which were probably *Comatula rotalaria* and *Comatula solaris*. The passage runs as follows:

> "In der Arafura-See habe ich im vorigen Jahre einmal 80 Exemplare einer grossen Comatula untersucht und fand circa auf jeder zehnten unsere Schmarotzer.... Alle dieser Myzostomen waren, wie die Comatula, weiss und schwarz gefleckt, und die ubrigen zahlreichen Schmarotzer des Thieres zeigten dieselbe Färbung."

The myzostomids found on the crinoids of Murray Island were very numerous and belonged to several different species. Dr. C. L. Boulenger, of Birmingham University, has been kind enough to undertake their identification. They are in many cases very brightly coloured and have pronounced colour patterns. Generally speaking, there are two types of pattern. In the first concentric rings of bright and dark pigment alternate. In the second the dorsal surface is ornamented with radiating ridges, and these are usually free from pigment or very light coloured. The ridges are thrown into relief by an edging of a dark pigment (*e. g.*, purple or black); the general ground colour between the ridges as a rule approaches that of the crinoid on which the parasite was found. One of these forms was very common on the dark green or black varieties of *Comanthus annulatum*. The alternate black and non-pigmented rings are in vivid contrast, but the myzostomid is thin and the non-pigmented parts are so transparent as to be inconspicuous against the dark ground of the host. This species seems to occur only on the darker crinoids. In another species the same arrangement is found, but much lighter hues prevail, green pigment alternating with very light brown. The colours of the host were, unfortunately, not noted.

When the host is very light coloured the alternation of darker rings does not occur. On a green variety of *C. annulatum* a specimen of Myzostma was found which matched it perfectly. The greater part of the body was bright green, but a few white spots represented a broken ring of a lighter colour; the edge was relieved by dashes of black pigment, while the cirri were brownish. A very magnificent example of the second type of colouration was secured on October 24, 1913, on a green form of *C. annulatum*. It resembled its host closely and was comparatively inconspicuous. The general colour was a bright green; the ridges appeared greenish white, darker at the edges owing to the addition of a granular pigment, and round each there was an intense black line. An allied form was found on darker crinoids; there the ridges were white or yellow surrounded by a darker line (in one case purple) and the ground colour was brown. Lastly, in one or two forms almost the whole upper surface may be covered by a dark pigment. Thus, is one specimen, the dorsum was a dark green, only relieved by a white line down the middle, while in another, the dorsum was purple. These occurred on dark crinoids.

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*von Willemoes Suhm, Zeits. f. wiss. Zool. Bd. xxvi, 1876.

On the whole, then, the myzostomids showed a great colour resemblance to their hosts, though (as in the preceding cases) striking exceptions occurred and, even when the colour schemes harmonised, protection from human sight at least was not always secured.

GASTEROPODA.

Two or three very small gasteropods, apparently parasitic, were found on the crinoids. While one or two were colourless, one individual (which occurred upon a very handsome crinoid striped red-brown and yellow) was very similar in colouring to its host. The shell was perfectly transparent, but the body was red-brown, with distinct yellow spots. Mr. G. C. Robson, of the British Museum, has kindly undertaken the description of this individual.

SUMMARY.

The object of this paper is to point out that of the large number of species belonging to many phyla which habitually shelter amongst the branches of the crinoids of tropical reefs, by far the greater proportion exhibit colour resemblance to the host. As the colour scheme of the host is often extremely variable (*e. g.*, *Comanthus annulatum*), that of the commensal, in some cases at least, varies too, but some commensals seem to be restricted in their response to the stimulus which causes this colour resemblance. Thus among the Crustacea, in *Synalpheus* all stages of variation are met with, according to the individual inhabited, between a pale form with very narrow stripes of pigment, to an extreme form totally covered with dark pigment; while in *Cirolana*, on the other hand, the individuals associated with even the darkest crinoids possess only insignificant lines of pigment on the otherwise totally white body. In the latter case there is, then, no protective resemblance, although we witness the incipient stages of its establishment. Other forms like the polychæt, the amphipod, and the brittle-star, *Ophiomaza*, give rise to dark varieties only and occur upon dark-green crinoids.

The following represents in a tabular form the results of the observations:

Commensal.	Pigments developed.	Host and colour variety of host.
Synalpheus brucei.............	Purple-black	All colour varieties of Comanthus annulatum and some other crinoids.
Synalpheus brucei.............	Red..................	Comatula purpurea.
S. comatularum...............	Brownish purple, purple and white.	All colour varieties of Comanthus annulatum and some other crinoids.
Cirolana lineata...............	Red or purple in faint thin lines, rest white.	All colour varieties of Comanthus annulatum and some other crinoids.
Cyclotelson purpureum.........	All purple..............	Dark varieties of C. annulatum.
Pontoniopsis comanthi.........	Bright green and black or yellow and red-brown.	Light (green or yellow) varieties of C. annulatum.
Periclimenes spp..............	Red and blue-purple.....	Dark varieties of C. annulatum.
Ophiomaza cacaotica............	Dark purple, brown or black.	Dark varieties of C. annulatum (one exception).
Ophiomaza cacaotica var. *picta*...	Black and white.........	Dark varieties of C. annulatum.
Ophiomaza obscura............	Dark brown and dull yellow.	Dark varieties of C. annulatum.
Polynoë minuta..............	Dark brown or black.....	Dark varieties of C. annulatum.

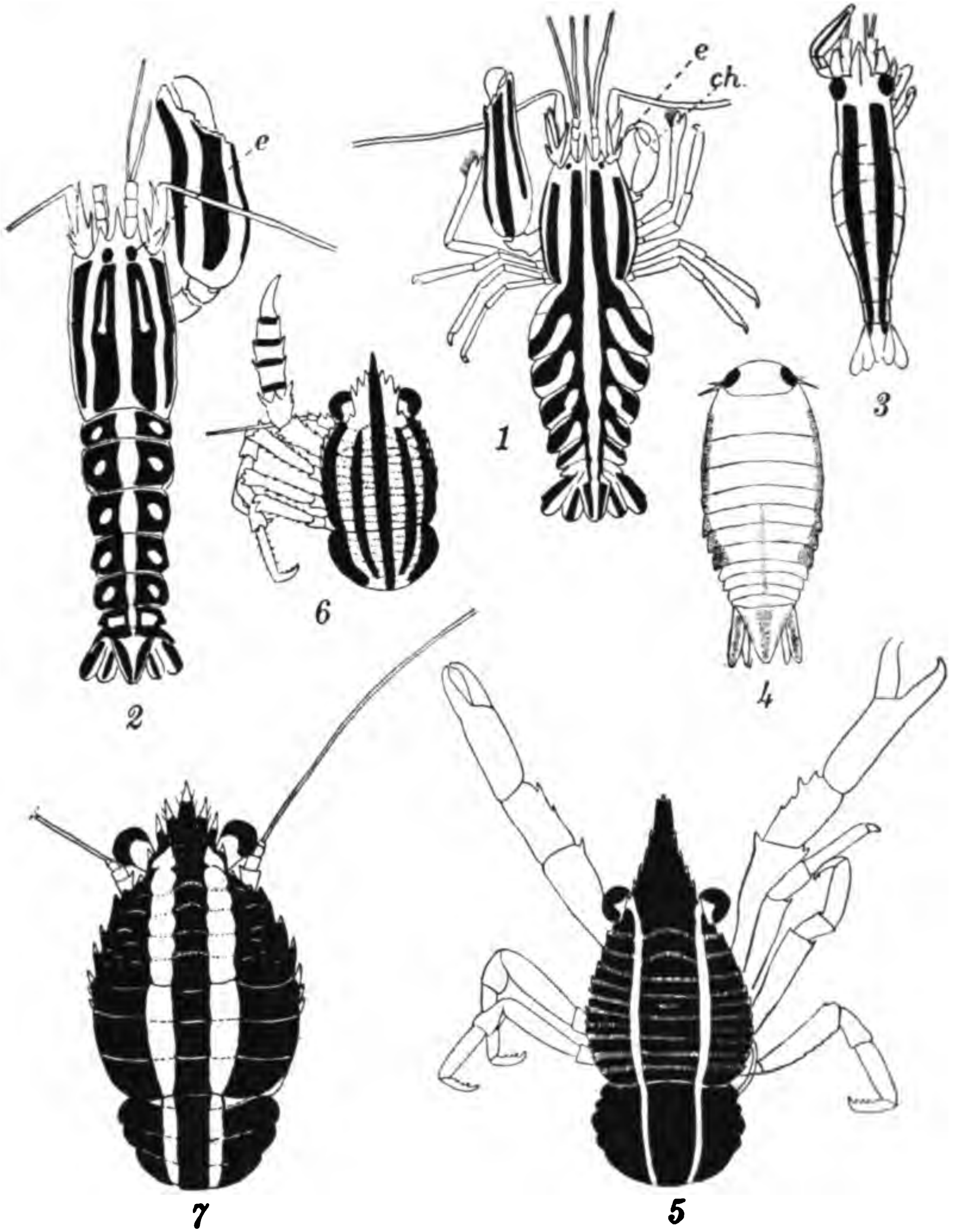

Fig. 1 *Synalpheus comatularum*. ×1.5.

Fig. 2. *S. brucei*: *e*, eye; *ch.*, small chela with its incurved thumb. ×3. Only a single example of *S. comatularum* and another of *S. brucei* is figured, so no idea of the variation in extent of pigmentation is shown, but only the type of arrangement. But both the type and variation are alike in the two species, that of *S. brucei* having rather deeper pigmentation, the bands being wider and the lateral unpigmented areas in the abdominal segments being completely enveloped by pigment.

Fig. 3. *Pontoniopsis comanthi*. ×6. Fig. 4. *Cirolana lineata*. ×7.

Fig. 5. *Galathea elegans*. ×4. Fig. 6. *G. minuta*. ×5. Fig. 7. *G. inflata*. ×6.

IV.

THE COMATULIDS OF TORRES STRAIT: WITH SPECIAL REFERENCE TO THEIR HABITS AND REACTIONS.

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THE COMATULIDS OF TORRES STRAIT: WITH SPECIAL REFERENCE TO THEIR HABITS AND REACTIONS.

By Hubert Lyman Clark.

INTRODUCTION.

In a paper on Recent crinoids, published a few years since,* our present generally acknowledged authority on that difficult group hazarded the opinion that "crinoids, as a class, are probably the most strictly sessile of all marine organisms," and further on he refers to them as "practically sessile organisms" as contrasted with star-fishes, brittle-stars, and sea-urchins. My own acquaintance with living crinoids was at that time confined to superficial observations on the European species of *Antedon* shown in the aquaria at Port Erin, Isle of Man, and at Naples, but I had carried away with me from those places the impression that comatulids are quite active animals, good swimmers, and anything but "sessile." When, therefore, I found myself a member of the party sent by the Carnegie Institution of Washington to Torres Strait, I determined, if littoral crinoids proved easily obtainable, to devote particular attention to their habits and reactions. My desire to do this was increased by the fact that in the paper to which I have referred, Mr. Clark makes statements with reference to food habits, bathymetrical distribution, size, and color of Recent crinoids, which seem to be based on assumptions rather than on observations, and from which he draws some far-reaching conclusions. It seemed clear that actual observations made on living crinoids, both in aquaria and under natural conditions on the reef, could not fail to be of interest and value.

It was fortunate, for the purposes of my investigations, that Dr. Mayer determined to establish our laboratory on Maër, the largest of the Murray Islands, at the northern end of the Great Barrier Reef, for comatulids of many different species and genera occur there and at least half a dozen kinds are common near low-water mark. It was therefore possible to make many observations from which certain deductions seem to be permissible. This report embodies those observations and deductions and necessarily includes some criticisms of Mr. A. H. Clark's assumptions. I hope, however, that these criticisms of his paper will not appear captious or irrelevant, since they are offered only with the desire of preventing erroneous assumptions from being received as proven facts.

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*The Recent Crinoids and their Relation to Sea and Land (Austin Hobart Clark, Geographical Journal, London, December 1908, pp. 602–607). This paper, except for its introductory paragraphs, is virtually a reprint, under another title, of the paper by the same author, in the American Naturalist for November 1908, entitled "Some Points in the Ecology of Recent Crinoids."

For the leave of absence which made my studies possible, it gives me pleasure to thank the authorities of the Museum of Comparative Zoölogy, while I also desire to express my obligations to my colleagues at the laboratory for much kindly assistance. Each member of the party made me his debtor, and I am glad to take this opportunity of thanking them for the help given in many different ways.

In order to give some idea of the richness of the comatulid fauna of Torres Strait, it seems desirable to give a list of the species collected. This list includes a number of hitherto undescribed species and must therefore include descriptions of them. The paper is accordingly divided into two parts, the first dealing with the comatulids from the systematic point of view and the second discussing their habits and reactions.

PART I.

THE COMATULIDS OF TORRES STRAIT.

The following list makes no pretensions to being complete, for it includes only the species collected by me in September and October 1913. All but three specimens were collected at Maër. The three exceptions, each representing a species, were taken on the sandy reef-flat on the southern side of Friday Island, September 13, 1913. The nomenclature and systematic arrangement here used (except in two or three insignificant details) are those of A. H. Clark's "Recent Crinoids of Australia" (Mem. Aust. Mus., iv, pt. 15, 1911) and later papers by the same author.

1. **Capillaster multiradiata** (L.).

A single specimen of this species was collected at Maër, just outside the reef, in about 5 or 6 fathoms of water. It was one of the very few specimens secured by means of a "tangle." The color in life was as follows: oral surface, black; dorsal surface, brown, the joints between the arm-segments much darker; whole dorsal surface, including the cirri, heavily silvered or frosted with white. The preserved specimen, dry, is light gray, the joints noticeably darker. There are 19 arms and the cirri are xxi, 20–24.

2. **Comatella nigra** (P. H. C.).

Two specimens of this species, well known from the East Indian region but not previously recorded from Australia, were taken on the outer portion of the southwestern reef-flat at Maër.

3. **Comatella stelligera** (P. H. C.).

This species is very common at Maër, especially on the southwestern reef-flat.

4. **Comatella maculata** (P. H. C.).

Common on both the southeastern and southwestern reef-flats at Maër, on the under surface of rock-fragments.

5. **Comatula pectinata** (L.).

Decidedly uncommon at Maër, but several specimens were taken with the following species. A single specimen was also taken on the sandy flat south of Friday Island.

6. **Comatula purpurea** (J. Müller).

Exceedingly common everywhere on the reefs about Maër. Very variable in color and size.

7. **Comanthus alternans** (P. H. C.).

A single specimen was collected by the diver, in 18 fathoms, outside the western reef-flat at Maër.

8. **Comanthus schlegelii** (P. H. C.).

Two specimens were taken by the diver, in 18 fathoms, outside the western reef-flat at Maër, and one specimen was found on the Great Barrier Reef itself on October 15.

9. **Comanthus annulatum** (Bell).

Exceedingly common at Maër; also taken on the flat south of Friday Island. Extraordinarily variable in coloration, ranging from lemon-yellow and brown to almost uniformly dead black, with bewildering diversity. One form is so sharply set off from the others that it is entitled to designation by varietal name and may be called var. *xanthum*. In it the dorsal surface is deep canary-yellow, while the pinnules are bright red. Only three specimens were found, all near the edge of the reef. Except for color, the specimens are not peculiar. Unfortunately the colors are very fugitive in alcohol.

10. Comanthus callipeplum sp. nov. (*καλλίπεπλος* = beautifully robed).

Centrodorsal moderate, flat, 5 mm. in diameter. Cirri viii, 15, about 7 mm. long. In addition to these rudimentary cirri, the margin of the centrodorsal has 10 large cirrus sockets. The small cirri taper to a slender tip. I Br and II Br series in close contact with the adjoining series of the same rank on either side, their dorsal surface smooth and nearly flat. Arms 78, about 90 mm. long and with approximately 100 brachials. II Br series usually 4 (3+4), but occasionally only 2. III Br series generally 2, but in one arm 3 and in two arms 4 (3+4). IV Br series 4 (3+4), except one arm which has 2. V Br series 4 (3+4). Syzygies between brachials 3 and 4, and 8 and 9, and then at intervals of three or four brachials. Outer brachials more or less overlapping with finely serrate distal margins. Lower pinnules on brachials rather short with 14 to 16 segments; distal pinnules notably longer and more slender, but with the same number of segments. Oral pinnules with 35 to 40 joints, but only the terminal fifth make up the comb. General color, dorsally dark green, with joints and some small spots greenish-yellow; sides of arms, including pinnules (and distally much of their dorsal surface), yellowish-white; centro-dorsal, partly white; cirri, yellow; tips of pinnules, usually rusty-red. Oral surface, very dark, but finely mottled with yellow-green. Colors little altered by preservation in alcohol.

This superb comatulid was found among madrepore corals near the outer edge of the southwest reef-flat at Maër. Only a single specimen was seen. Although nearly related to *C. briareus* (Bell), it is distinguishable by the presence of cirri, the great breadth of the II Br series, the absence of interradial plating, the frequent syzygies, and the remarkable coloration. The specimen was kept alive in the laboratory for nearly 24 hours, while a colored figure was being made, but it died and broke to pieces before preservation and is now in an unfortunately fragmentary condition.

11. Comanthus luteofuscum sp. nov. (*luteofuscus* = yellow-brown).

Centro-dorsal small (2 mm. in diameter of bare surface), thick, flat, or a trifle concave. Cirri xviii–xxii, 13–17, rather short, about 10 mm. long. Except segments 4–7 (from the base), the cirrus-segments are short, wider than long; except 7 or 8 basal segments, each segment has a dorsal elevation of more or less prominence; this may be a tubercle, a spine, or a rough transverse ridge; it is often conspicuous. I Br series 3 (2+3); I Br$_1$ in close opposition with its adjoining fellows; I Br$_2$ notably wider than I Br$_3$ and in broad contact with its fellows; I Br$_3$ almost triangular, very low and broad, well separated from its fellow on either side. Arms 20 to 30, notably short, 50 to 60 mm. long, usually approximately equal but sometimes distinctly longer on one side of the animal than on the other; each arm is made up of 80 to 100 brachials, which, except at tip of arm, are low, more or less discoidal, and have everted and finely serrate distal margins, particularly near middle of the arm. II Br series generally 4 (3+4), but occasionally 2. II Br$_1$ in close contact with its fellow of the same ray. III Br series generally 4 (3+4), but sometimes 2. III Br$_1$ in contact with its fellow of the same half-ray. First brachials in similar contact. Syzygies between brachials 3 and 4, and 10–11 or 11–12; after that at intervals of 3 to 5 segments. Oral pinnules with 30 or more joints, of which 8 or more make up the comb. Arm-pinnules of only a dozen joints; even the distal pinnules are short; those at base of arm and near middle are stout and the joints have everted and finely serrate distal ends. General color in typical specimens, bright yellow-brown; in some cases this is very much darkened and has a greenish cast; rarely the tips of the arms are green or greenish-yellow. Colors are well kept in alcohol.

This pretty little comatulid was not at all rare on the reef-flat at Maër, but it was nowhere abundant. It is obviously closely allied to both *parvicirrum* and *annulatum*, but is readily distinguished by the short arms, the well-developed and numerous cirri, the character of brachials and pinnules, and the distinctive coloration.

12. **Comanthus parvicirrum** (J. Müller).

This is one of the loveliest crinoids found at Maër, but is not at all common. The specimens taken were found on the under side of rock-fragments. The typical coloration is rose-red and white. Unfortunately the colors are very fugitive in alcohol.

13. **Comanthus samoanum** (A. H. Clark).

Only a few specimens of this species were found. They occurred with, and were not recognized as distinct from, *annulatum*, but can now be distinguished without difficulty.

14. **Stephanometra monacantha** (Hartlaub).

A single specimen was taken on the southwestern reef at Maër on October 11. It was an active and very graceful swimmer.

15. **Stephanometra stypacantha** sp. nov. (*στύπος* = stick + *ἄκανθα* = spine).

Centro-dorsal large, thick, slightly convex, almost completely covered by the cirri; its diameter is 3.5 mm., but its bare surface is less than a millimeter across. Cirri XXXIII, 18, about 12 to 13 mm. long, distally very distinctly compressed; basal 3 or 4 and terminal half dozen segments more or less shortened, the others longer than wide; terminal six or seven may show a longitudinal keel dorsally, but this is never marked; opposing claw distinct but small. Arms 16, about 70 mm. long, slender and well separated; division series all 2, without syzygies; axillaries pentagonal, nearly as long as wide; no lateral processes and no tubercles; brachials quadrate at base of arm and distally, but 7 to 30 (or thereabouts) more or less markedly wedge-shape; syzygies between 3–4, 16–17 and then at intervals of 6 to 8 joints; sometimes between 9–10, 14–15 (or 15–16) and then at intervals of 5 or 6 joints. P 1 about 4 mm. long, flagellate, with 14 joints, the basal ones stout, but distal ones long and very slender; P_a similar but much smaller. P_2 very rigid, 8 mm. long, sharp and spine-like (hence the name selected), consisting of 9 joints, of which 3 to 6 are greatly elongated (3 times as long as thick, or more) and 9 is minute; P_b similar, but evidently smaller in every way; P_3 similar to P_2, but only 5 or 6 mm. long; P_c similar but much smaller; P_4 more flagellate, less than 3 mm. long and with only 8 joints; P_d similar and about equal to P_4; succeeding pinnules gradually becoming longer, but not exceeding 6 or 7 mm. and with 14 or 15 joints; all pinnules more or less cylindrical and with smooth joints. Color, uniform deep red-purple, except cirri, which are nearly dull-yellow at base and only dark at tip. The color is well kept in alcohol, except that light spots at base of arms and distally are now visible, which were not noted in life.

This species seems to be very well characterized by the numerous, few-jointed, nearly smooth cirri, the absence of ventro-lateral processes on the arms, and the small number of segments in P_2. The form and proportions of the lower pinnules also seem to be characteristic. Only one specimen was secured. It was found among the corals on the southwestern reef at Maër. It was noted as an active swimmer and did not endure confinement well, soon throwing off its arms.

16. Lamprometra tenera (Hartlaub).

A single specimen was taken on the southwestern reef at Maër, September 26, 1913. It was an active and very graceful swimmer. The lower pinnules are stouter and the coloration more variegated and much handsomer than in specimens of *tenera* from the Marshall Islands.

17. Lamprometra brachypecha sp. nov. (*βραχύς* = short + *πῆχυς* = arm).

Centro-dorsal large, thick, flat, 5 mm. in diameter, the base dorsal area about 2.5 mm. across. Cirri XXXVI–XLVI, 22–25, distally compressed, all joints wider or higher than long; distal joints with a very inconspicuous and low longitudinal ridge; opposing claw very small. Arms 39 to 50, notably short (hence the name selected), 50 to 60 mm. long and 10 to 12 mm. wide distal to the middle, composed of about 100 joints; no lateral processes and no tubercles; basal brachials are slightly swollen either at middle or at distalmost corner; first few brachials nearly quadrate, but rapidly becoming low wedge-shape, twice as wide as high, and then gradually becoming quadrate again as the tip of the arm is approached; syzygies between 3 and 4, 15–16 (or 18–19) and then at intervals of 9 to 19 (usually 10) joints. Division series all 2, without syzygies; there may be as many as 10 IV Br series, but they are not necessarily on outer side of arm. Lower pinnules on outer side of every first and fourth arm, much bigger than any others. P_1 usually about 10 to 12 mm. long, with 23 or 24 joints, more or less cylindrical and stiff, but somewhat flagellate at tip; P_a about the same. P_2 bigger than P_1 to a greater or less degree, often 13 or 14 mm. long and with 25 joints; P_b similar but smaller. P_3 very small, not half of P_2, with 8 to 11 joints; P_c about the same. Succeeding pinnules gradually becoming longer and at middle of arm, 6 to 8 mm. long and composed of 19 or 20 segments. All pinnules more or less cylindrical and with perfectly smooth joints. Color, bright green, somewhat variegated with brown and white, and with a broad band of white crossing each arm distal to middle; this band is particularly marked on the oral surface; between this band and the disk are 3 or 4 narrow bands of green; pinnules, at least distally, with yellow tips. The colors slowly undergo some change in alcohol, but the pattern is well preserved.

In many respects this was the most remarkable crinoid met with at Maër, but unfortunately it was rare and only four specimens were found. They were all taken on the under surface of rock-fragments on the southeastern reef-flat. It was not an active species and I did not see it swim. When the rock was overturned, the arms would be more or less closed over the mouth, the whole animal appearing like a tuft of green sea-weed. On being touched, however, the arms, instantly and all together, were laid back flat against the rock and the broad white band flashed into view. The immediate effect was obliterative and one's first thought was that the animal had vanished. Whether this habit is protective could not be determined from the few observations possible. There is no doubt this species in near *lævicirra*, but the small size, short arms, numerous, fewer-jointed cirri and the color are all distinctive. There is a faded specimen in the M. C. Z. collection, from Fiji, which seems to be *brachypecha*.

18. Lamprometra callipecha sp. nov. (*καλλίπηχυς* = having beautiful arms).

Centrodorsal rather small, flat, less than 5 mm. in diameter, the bare dorsal area about 3 mm. across. Cirri XXXI, 23–25, about 12 mm. long, distally compressed; basal segments (1 to 3) short and thick, segments 4 to 8 longer than wide, remainder wider than long; distal segments with low and minute longitudinal dorsal ridges; opposing claw well-marked. Arms 18, about 65 mm. long by 10 broad; division series all 2 without syzygies; there are four II Br series and four III Br; II Br series not appressed, but with slight lateral expansions; brachials smooth, not overlapping, wedge-shape, becoming quadrate after the 30th, and at tip of arm longer than wide; syzygies between 3–4, 9–10, 14–15, 18–19, 23–24, and then at intervals of 7 to 10 segments. All pinnules cylindrical; lower ones stiff and little flagellate. P_1 about 6 mm. long, of 19 joints; P_a much smaller, little longer than P_3, of 11 joints. P_2 the largest pinnule, 7 or 8 mm. long, of 18 joints; P_b longer than P_a, of 11 joints; P_3 the smallest pinnule, of 10 joints; P_c very similar. Succeeding pinnules gradually increasing in length until at middle of arm they are 6 or 7 mm. long, with about 20 joints. Color, rich purple, with base of arms and a broad distal band white; pinnules often with yellowish or rusty tips; cirri, cream-color dorsally, deep brown on ventral side. Colors almost perfectly preserved in alcohol.

A single specimen of this very handsome comatulid was found on the southwestern reef at Maër on the last day of our stay, October 27, 1913. It is well characterized by the small number of arms, the number and appearance of the cirri, the proportions of the lower pinnules, and the notable coloration.

19. Oligometra anisa sp. nov. (*ἄνισα* = unequal; hence, variable).

Centro-dorsal moderately large, but notably thick, about 5 mm. in diameter, the bare dorsal area about 2 mm. across and minutely tuberculated. Cirri XXI–XXIII, 15–17, relatively long (9 or 10 mm.) and stout; transverse ridges on distal joints minute or wanting but opposing claw marked; none of the segments obviously longer than wide. Arms 10, the I Br series and first 2 brachials with well-marked ventro-lateral processes. First half dozen brachials more or less quadrate; succeeding, wedge-shaped, with flaring and slightly overlapping distal ends, becoming quadrate and longer than wide at tip of arm; syzygies between 3–4, 9–10, and then at intervals of 5 to 7 segments. All pinnules more or less cylindrical. P_1 about 7 or 8 mm. long, of 10 or 11 joints, moderately stiff; P_a similar but often distinctly larger. P_2 and P_b about equal, distinctly the largest and most spike-like of the pinnules, of 13 to 15 joints, with rough and spiny distal ends. P_3 much shorter than P_2, but rather stout, of 10 or 11 joints; P_c smaller, of only 8 joints. P_4 the smallest pinnule, much shorter than P_3; P_d nearly equal to P_c. Succeeding pinnules gradually longer, until at middle of arm they are 6 mm. long and have about 20 segments. Color, very variable, ranging from clear lemon or canary-yellow, with hardly a purple mark, through variegated purple and yellow, or variegated brown and white, to finely variegated shades of gray and white. Colors are well preserved in alcohol.

Excepting the comasterids, this was the commonest crinoid at Maër and was not infrequently met with near the outer margin of the southwestern reef-flat. Unfortunately it was not common enough to permit of any extended observations on its habits and reactions. It was not ordinarily at all active, but clung very tenaciously to the fragment of rock or coral to which its cirri attached it. The cirri are notably strong and it was frequently no easy task to detach them. Although no doubt related to *O. carpenteri*, this species is readily distinguished by the more numerous cirri, with fewer joints; the shorter arms with about half as many joints (80 in *anisa*); and the utterly different lower pinnules.

20. Heterometra delicata sp. nov. (*delicatus* = soft, tender).

Centro-dorsal relatively large, 2 mm. in diameter, low subconical, only the dorsal pole bare. Cirri XV, 18–19, little compressed distally, about 5 or 6 mm.

long, rather stout; no segments longer than wide; 10 to 12 distal segments with conspicuous longitudinal dorsal crests or teeth; opposing claw large. Arms 10, the I Br series and first two brachials with small ventro-lateral processes. Arms about 25 mm. long, composed of about 50 to 60 brachials, which are more or less quadrate and are distinctly longer than wide on distal part of arm; syzygies between 3–4, 9–10, and then at intervals of 6 to 9 joints. P_1 less than 2 mm. long, composed of 10 or 11 short joints, the basal ones squarish; P_a similar but much smaller and with only 6 segments. P_2 similar to P_1 but more than 2 mm. long, rather stout, with 10 joints, decidedly the largest pinnule on the arm; P_b about equal to P_1 or a trifle larger, but with fewer joints; distal edges of segments of P_2 and P_b somewhat flaring, very minutely spiny. P_3 smaller than P_1 and with only 6 joints; P_c similar but smaller. Succeeding pinnules gradually larger, until at middle of arm they are about 3 mm. long and have 12 segments. None of the basal pinnules are rigid and spike-like, but all have rather flagellate tips. Color, purple of a rather pale shade; pinnules yellowish at tips; cirri more or less white. Colors fairly well preserved in alcohol.

The single specimen, upon which this species is based, was picked up on the sand flat, on the southern side of Friday Island, at low tide. Its relationships are obscure, for although it seems to be a member of the Himerometridæ, the outer brachials preclude its being placed in *Amphimetra*, while the known species of *Heterometra* all have more than 10 arms. It may perhaps need a generic name of its own.

21. Tropiometra afra (Hartlaub).

Not common, but a few specimens were found on the extreme outer margin of the southwestern reef-flat at Maër.

22. Iridometra nana (Hartlaub).

A very active comatulid, purplish-black with light brown cirri, was taken on the southwestern reef at Maër, October 10. The arms are 40 to 45 mm. long. It is apparently an *Iridometra*, and, except for the distinctive color, which is well preserved in alcohol, it answers well to Hartlaub's description of *nana*.

PART II.

HABITS AND REACTIONS.

MATERIAL.

Crinoids are so abundant and easily obtained at Maër that there was no lack of material for study, but experience unfortunately showed that the species with which the most interesting results might have been obtained were so uncommon as to be unavailable for experimental work, while the most abundant species were very sluggish and often unsatisfactory to deal with. Moreover, individual differences were quite marked, more so than I had expected, and led of course to inconsistent results. The commonest comatulids, the young individuals of *Comatula purpurea*, proved less satisfactory for experimental work than adults of the same and of larger species, as they are rather inert, responding slowly to stimuli; but many observations were made on their behavior under normal conditions on the reef. Most of my observations and nearly all the experiments at the laboratory were made on adult *Comatula purpurea*, *Comatella maculata* and *stelligera*, and *Comanthus annulatum*. Of these, the last was the most easily available, but it was not so active as the others. Everything considered, adults of *Comatula purpurea* were found the most satisfactory for purposes of study, as their responses to stimuli seemed to be more prompt and more marked than in any other individuals, and the results were more consistent. Unfortunately these available comatulids are all members of the family Comasteridæ and had many traits in common. The comparatively few individuals of the families Stephanometridæ, Mariametridæ, Colobometridæ, and Antedonidæ, which I had the chance to watch, showed that they differ from the Comasteridæ as much in habits as in structure. They are good swimmers and would be exceedingly interesting to study critically in the laboratory.

All but two of the crinoids seen by me were found either on the lower surface of rock-fragments or among the branches of stony coral of various species. They occurred on different parts of the reef-flat about Maër, but except the ubiquitous *Comatula purpurea*, they were virtually confined to the southern end and eastern side of the island. They were usually in water not less than 2 or 3 feet deep at low tide, but occasionally when the tide was very low they were in water only a few inches deep. Twice specimens were found in the cavities of large sponges, and it is possible that outside the reef this may be a common habitat. Owing to the lack of facilities for dredging, no observations were possible on crinoids living in the deeper water beyond the reef.

It was a pleasant surprise to find that with few exceptions the crinoids at Maër were not nearly as delicate and frail as their exquisite texture would lead one to suppose. Unless the arms were voluntarily ruptured, they were not easy to break, and even pinnules and cirri withstood hard pulling, when specimens were being untangled from each other. The arms were seldom voluntarily ruptured until the specimens had been in the laboratory for some hours, and if properly supplied with fresh, clean water, individuals could be kept for a day or more. The diversity of color, the delicacy of structure, and the gracefulness of movement surpass description and easily justify Mr. A. H. Clark's statement (1908, Geog. Jour., London, p. 606) that among marine invertebrates they are unrivaled. They may well be called "sea-lilies," for nothing outside the most beautiful products of the vegetable kingdom can be compared to them for beauty.

METHODS.

It proved impracticable to have aquaria at the laboratory large enough to keep comatulids in a healthy condition, but a compartment in the live-car anchored just outside the reef served as a home for numerous specimens, available for experiment either at the car or at the laboratory. Crinoids kept in the car for many days lost the terminal portions of some or all of their arms, apparently because of the constant swaying of the car, and during the last week of our stay a particularly rough night killed nearly all the comatulids in the car. For observations and experiments at the laboratory, a tank or trough 3½ feet long, 10 inches wide, and 10 inches deep, made of metal and wood, answered very well. This will hereafter be referred to simply as the *tank*.

As only a part of the time could be given to the work, even for the short period we were at Maër (five weeks), no attempt was made to secure quantitative results. Consequently only superficial attention was given to variations in the strength of stimuli or in rapidity of response. The purpose was simply to learn how comatulids reacted under normal conditions, so that such observations as were made on responses to chemical stimuli were purely incidental. Of course, observations were continually made on the reef and some experiments were undertaken there, but various circumstances combined to make the results negative. Had more time been available, even another week, I would have been able to profit by the experience of some of these failures, but as it was they were of very little significance, although they will be referred to further under the discussion of locomotion. Like other students of animal behavior, I found individual differences sufficiently marked so that selected specimens gave the best results. After a number of specimens had been observed and frequently disturbed, one or more were picked out, which seemed most responsive, and the more careful observations were made on them. There is no reason for believing such observations unrepresentative, for these selected specimens did not differ, so far as could be seen, in the manner of the response, but only in the rapidity. Handling individual comatulids had no apparent subsequent effect on the specimen.

Fatigue seems to be, as a rule, easily induced, but in no other respect is there so much individual diversity as in this. Whether the fatigue noted was real or only apparent, there was no means of determining. Nothing was noted with reference to breeding habits. Dr. Tennent found mature spermatozoa in many males of *Comatula purpurea*, but mature eggs were not noted in any species. Apparently the breeding season was just opening when we came away, the last of October. The shortness of our stay prevented any observations on regeneration or growth. In the following pages, under the heads *locomotion*, *food and feeding*, *response to light*, *response to heat*, and *response to other stimuli*, the facts observed are set forth.

LOCOMOTION.

To speak of the methods of locomotion in crinoids, or even in comatulids, is like speaking of locomotion among birds, in that there is as much difference between different kinds of comatulids as between different kinds of birds, and as birds may either fly or run preponderatingly, so comatulids may either commonly swim or creep. So far as the species studied at Maër are concerned, the Comasteridæ are creepers, while the other families represented there are swimmers. It was a surprise and disappointment to discover that none of the common comatulids would swim, even in the deep water by the live-car, so that it was not possible to make the observations and experiments with reference to the swimming of comatulids which I had planned. When any of the species of the Comasteridæ were placed in the water beside the live-car, they invariably sank to the bottom (about 20 feet). In the case of *Comatella maculata*, it was noted that, as a rule, the individual would close the arms orally and vertically over the disk, so that it sank almost like a stone. As soon as it touched bottom, the arms were opened out and the animal began to creep. In the other species, however, the arms were not closed up and so the comatulid floated downward to the bottom much more gradually. With one exception, all efforts to induce swimming movements of the arms in a comasterid completely failed.

In no case when the individual was on the bottom did mechanical stimulation result in any attempt to swim or in accelerated movements of any kind. Suspending specimens in the water by means of a slender thread gave no results; the arms moved about slowly and with no coördinated effort and with no resulting locomotion. Several individuals were provided with cork floats, so attached as not to interfere with arm-movements; but, with the one exception already referred to, none of them made any effort to swim. The one exception was a small *Comatella maculata,* which, after wearing the cork float in the live-car for 24 hours, was dropped into deep water. It immediately began swimming, but spasmodically and not in the beautifully coördinated manner of a *Stephanometra.* Apparently these comasterids do not, under normal conditions, swim at all, but could with sufficient effort be taught to do so.

On the other hand, all of the species of the other families of comatulids observed at Maër are good swimmers and do not creep about as the comasterids do. They are usually found at rest on the lower side of rock-fragments or on a branch of coral with the arms more or less erect, but sometimes the arms are opened out flat against the rock. They maintain their position by means of the cirri, with which they often cling so tightly that it is difficult to dislodge them without damage. Under no conditions did they seek to escape by swimming, but when once dislodged, swimming seemed to be their only means of locomotion. Placed in a basin or a deep bucket of sea-water, a very slight mechanical stimulus served to set them in motion, and swimming continued for a more or less brief interval, varying greatly with different individuals. It seemed as though the frequent contact with the side of the basin or pail served as a deterrent, and I think that they would undoubtedly have gone a greater distance in open water. Nevertheless it was clear that the individuals observed were "sprinters," and not long-distance swimmers, the movements being more like the flitting of small birds in shrubbery than like long-sustained flight. The gracefulness and beauty of the movements were their most notable feature, but their rapidity and force were also remarkable.

In the ten-armed specimens, swimming was accomplished by using the arms in sets of five alternately, so that when arms 1, 3, 5, 7, and 9 were brought up almost vertically over the disk, arms 2, 4, 6, 8, and 10 struck backward forcibly, with pinnules fully extended, until they nearly met behind the cirri. Only a single stroke was made, but as arms 2, 4, 6, 8, and 10 were relaxed and drawn in and upward over the disk, another similar stroke was made by the alternating five arms. Of course the movement was much more rapid than a description indicates, but it decreased in rapidity as the comatulid became fatigued. At the start the strokes were at the rate of perhaps 100 per minute, but they rapidly dropped to much less than that and usually ceased altogether in less than a minute. Each stroke appeared to carry the individual about the length of its own arms, so that an individual with arms 50 mm. long started out at the rate of about 5 meters per minute. But the longest distance any specimen was seen to travel continuously was less than 3 meters.

In the multibrachiate Stephanometridæ and Mariametridæ, the movements were very similar, but exceedingly difficult to analyze satisfactorily. The arms seemed to be used in sets of five in rapid succession. That is, supposing the individual had 40 arms, the first stroke would be given by arms 1, 9, 17, 25, and 33, followed almost immediately by 2, 10, 18, 26, and 34, then 3, 11, 19, 27, and 35, and so on until the eight sets had been used, when the first set would come into action again. Not so great a part of each arm is used as in the ten-armed species and the stroke does not carry the arm so far back, but the movements are so rapid and the similarity of the arms to each other is so confusing that it is almost impossible to feel sure that one has made no mistake in the analysis of the method of progression. While the swimming is perhaps just as graceful as that of the ten-armed species, when contrasted with their movement, it is reminiscent of "dog-paddle" swimming as compared with the usual stroke. No satisfactory data were secured regarding the speed of, or distance covered by, the multibrachiate species.

The creeping movements of the Comasteridæ are neither so graceful nor so well coördinated as the swimming movements just discussed. These comasterids usually live in the open spaces among branching corals or on the lower side of large fragments of rock or coral, with their arms extended and floating listlessly in the water. More or less constantly but irregularly the arms bend inward toward the mouth, the tips just brushing the disk and the arm-bases. While these movements may be connected with feeding, it was not possible to determine what the connection is. One may perhaps hazard the guess that they keep the ciliated grooves from becoming clogged up. If the coral is broken away or the rock fragment turned over, so that the comatulid is exposed, the animal begins at once to move. In the species with well-developed cirri, notably in *Tropiometra afra* Hartlaub, the position is maintained by means of them, but they apparently do not play any important part in locomotion. One might suppose that they would be of some use either in pulling or pushing, but there never was the least indication of movement on the part of the cirri in any of the species observed. In the species in which cirri are feebly developed or quite wanting, the position is maintained by the use of some of the arms. It seemed to be usually the shorter arms that were so used, but under laboratory conditions none of the arms remained still for a long period, and while it would seem quite likely that the shorter arms are constantly used as anchors, evidence on the point is not satisfactory.

Creeping is a rather complex movement, a combined pulling and pushing. Certain arms, usually three or four but sometimes as many as seven, are stretched out to their full extent and the pinnules of the terminal portion catch hold of any available projections. This attachment is not only by the use of the minute hooks which are found at the tips of the pinnules, but by the remarkably viscid nature of the secretion from the glands in their epithelium. The degree of viscidity varies in the different species and more or less in individuals. It is least noticeable in *Tropiometra afra* Hartlaub and hardly more so in *C. purpurea.* It is most marked in *Comatella stelligera* and in some individuals of *Comanthus annulatum.* Thanks to this viscidity, locomotion is possible even on very smooth surfaces, such as that of an enamel-ware basin. It is, however, difficult on loose sand. Rock surfaces and tightly packed sand are the most satisfactory for permitting the pinnules to function successfully. When the pinnules of the extended arms have gotten a hold, or perhaps while they are getting hold, three or more arms on the opposite side of the body are drawn up in a strongly arched position and their widespread tips are closely appressed to the bottom very near the disk. Then when the extended arms, having secured their hold, begin to contract and *pull* the animal towards the place of attachment, the arched arms begin to straighten out and *push* the animal in the same direction. The result is of course a movement more or less marked according to the character of the bottom and the size of the comatulid. The total movement may be from one-eighth to a quarter of the arm-length. The process is continually repeated and may be kept up for hours, with very slight resting periods.

On the whole, *Comatella maculata* and adult *Comatula purpurea* were the most active and were rarely at rest in aquaria. A specimen of *maculata* with arms about 75 mm. long traveled approximately 85 mm. per minute and continued to go around and around a large basin for several hours. It probably traveled about 40 meters per hour, but on a natural surface, such as the reef would afford, it would be able to do better than that. In comatulids with approximately equal arms, there was no evidence of any orientation, one group of arms being quite as likely to be in advance as another. Such individuals altered the direction in which they traveled simply by changing the groups of arms which were to be extended.

In adult *Comatula purpurea,* as is well known (the same is true of many comatulids not found at Maër), certain arms are much longer than others, and the shortest are as a rule opposite the longest. Observation on the reef, at the live-car, and at the laboratory showed that in this species there is more or less definite orientation. Under ordinary conditions the long arms are extended in locomotion and hence are *anterior,* while the short arms do the pushing and hence are *posterior.* The mouth is at the base of the longer arms and hence is at the anterior end (or side) of the animal, as one would expect. If locomotion in a given direction were prevented, the comatulid never reversed its movement, using the short arms to pull and the long ones to push, but gradually swung itself around until ultimately the long arms were in advance. A considerable number of experiments and observations showed that the mechanism for orientation was not by any means perfectly adjusted, for an individual would often go for some distance with the longest arms at one side or only partially in front. Nevertheless it was clear that long arms in front, short arms behind, gave the normal method of progression. It may be a fair inference that the asymmetrical condition of the arms is the result of selection, since it is possible that long arms would be better for pulling and short, stout arms for pushing. But it is no doubt true that there are very diverse interpretations of the matter possible, and it is no part of my purpose to discuss the subject here. The statement of the facts given above is beyond dispute, however.

Locomotion in all the comatulids observed at Maër, whether swimming or creeping, invariably takes place with the oral surface uppermost. If dropped in deep water with the mouth down they commonly righted themselves before reaching the bottom. If not, or if placed on the bottom with the mouth down, they slowly but surely turned over before attempting to either swim or creep. The process of turning over is essentially the same as in a starfish. That is, a group of arms begins the task and continues gradually lifting up one side until the arms of that side can be bent back far enough over and beyond the aboral surface to secure a hold. Then by their pulling and the pushing of the arms opposite to them, the disk is righted. The process seems a tedious one and is probably not often necessary in the normal life of comatulids on the reef.

Particularly interesting is the question of how much these comatulids move about under the natural conditions of their life, but no satisfactory evidence on the point was secured. On one occasion a dozen healthy comatulids of four species were "planted" on a part of the reef where no crinoids were living. Twenty-four hours later they had all disappeared and no trace of them could be found in the neighborhood. But as there had been a strong wind and much surf during the night, they may have been simply swept away. On another occasion 10 large comatulids were carefully located around the margin of a rock-fragment about a meter in diameter. Circumstances, including unfavorable tides, made it impossible to visit the spot again for a week. Then it was found that more or less sand had washed in around the rock and the comatulids were apparently gone, but again there was doubt what part the surf and strong tidal currents may have played. Crinoids dropped beside the live-car, on reaching the bottom, began at once to move away and continued moving, usually in a fairly straight line, until they reached a rock beneath which they could find shelter, but it was not possible to determine their ultimate resting-place.

During these experiments I was much struck by the attitude of fishes towards the crinoids. Fishes of many species were abundant in the water just outside the reef and their movements were easily noted. Any object dropped in the water at once attracted their attention and if edible was nibbled at or seized outright. Comatulids were always noticed, but were never touched either in the water or at the bottom. Fishes, often of large size, always swam towards them, but when within a few inches turned and swam away. Either by sight, or some other sense, perhaps stimulated by some exhalation from the comatulids, these animals were recognized as inedible.

FOOD AND FEEDING.

Examination of the contents of the stomachs of living crinoids were made on two different occasions. One day two crinoids, which had been in the live-car for several days, were brought to the laboratory and the contents of their stomachs were carefully examined under the microscope. No essential difference between the two specimens was noted. In each case, the greater part of the food material was green algæ, chiefly unicellular, but some linear forms (thread-algæ) were also noted; a few diatoms were detected and some foraminifera; in one of the stomachs, several radiolarians were also seen. There was no indication that other than living food material had been taken into the stomach. All of the material was virtually undigested. On another day a study was made of the contents of the stomachs of two crinoids just brought into the laboratory from the reef. In both individuals the food material was identical with that of the crinoids which had been living in the live-car. In one specimen a piece of a red alga was noted and in the other some fragments of minute crustacea. These last were the only particles of animal food noted and were the only things observed that could possibly have been taken in as dead plankton. It was made perfectly clear that the comatulids at Maër, at least in the dry season, are all vegetable feeders, and that the percentage of animal food is negligible. But it is possible, of course, that during the rainy season there may be a change in the composition of their diet; on that point there is no evidence to offer.

It is not easy to determine beyond question the manner in which the food reaches the stomach. It *is* easy to *suppose* that the food is simply swept into the mouth by the current of water flowing along the ciliated furrows of the arms and disk, but I did not succeed in demonstrating such a movement, although there is no reason for doubting its reality. The multibrachiate forms keep the arms more or less widely spread out when they are at rest, but in the ten-armed species they are often more or less erect and sometimes quite rigid. In the aquaria and live-car the arms are frequently if not constantly curving in towards the mouth and the tips sweep the surface of the disk lightly. Individuals living on the lower surface of rock-fragments, since they are attached by the aboral side, rest with the ciliated grooves and mouth downward, away from the surface of the rock. It is therefore evident that, unlike starfishes and echini found in similar situations, they get their food from the water directly and not from the surface on which they rest. Taking all the facts observed with reference to the nature of the food, the position and movements of the arms, and the arrangement and appearance of the ciliated furrows, it is evident that the comatulids at Maër obtain their food, living vegetable plankton, directly from the sea-water by means of the ciliated furrows and that the arms serve no essential purpose *in feeding* other than the multiplying and extending of these furrows.

If this view is correct, a plentiful supply of sea-water containing an abundance of the necessary plankton would be the essential factor in controlling the distribution of these comatulids, and their local occurrence about the island might throw some light on the matter. The island of Maër is surrounded on all sides by a fringing reef between which and the shore itself is a reef-flat of great extent, as much as 600 yards wide on the southeast side of the island. The reef is lacking only at one point, the west-south-west corner of the island, but it is nearly wanting at the southern point also. Between these two gaps the southwestern reef is very rich in corals and in other animal life. Directly across a channel, about a mile wide, lie the islets Dauer and Weier, also surrounded by an extensive fringing reef. Through this channel the tidal movement is very marked, spring tides at the Murray Islands rising not less than 10 feet. On the southeastern reef there is constant surf breaking (at least during the southeast trades of the dry season), but the tidal movement on the flat itself is not particularly active. At the northern end and on the west side of the island, neither surf nor tide is as marked as on the other side.

We examined the reef and the reef-flat on all sides of the island and were constantly searching for crinoids. Young *Comatula purpurea* were found practically everywhere in water that was well aerated, but no large comatulids were found anywhere on either the western or northern parts of the reef. On the southeast reef-flat, *Comatella maculata* was fairly common and occasionally a *Comanthus annulatum* or a *Lamprometra* would be found there; but we soon learned that when we wanted crinoids in any numbers, the southwestern reef was the place at which to obtain them. They occurred there in great abundance, and especially near the outer margin of the reef the number of species and the size of the individuals were notable. A natural explanation of this fact is that the great tidal movements through the channel between Maër and Dauer maintain a richer supply of vegetable plankton at that point than is to be found on any of the other reefs. It may be added that the abundance of food is, as will be shown later, only one factor in making the southwestern reef so attractive to comatulids.

RESPONSE TO LIGHT.

Almost the first fact noted with reference to the habits of the comatulids at Maër was that they showed an evident tendency to withdraw from brightly illuminated areas. On overturning a rock-fragment on the lower surface of which crinoids were living, they at once began to move. Sometimes they withdrew into dark holes or crannies in the rock, but generally the movement was over the surface of the rock to its margin and thence down into the shade of its now lower side. The movement was never spasmodic or hurried, but unless interfered with was very steady and soon accomplished its purpose. It is difficult to see how this invariable habit can be interpreted as anything else than a response to light as a stimulus. Since the rock might be 3 feet under water, no change of temperature could possibly have caused the movement; it is conceivable, however, that the change of position due to the overturning of the rock was the effective stimulus. But the theory that change of position is the determining factor seems to be eliminated by the facts that among the living corals comatulids occur with the oral surface either up, down, or lateral, and that when the coral around them is broken away with a hammer, exposing them to strong light but not disturbing their position, their movements are also away from the lighted area into the shadow.

Experiments in the laboratory were not altogether satisfactory, so much individual difference was shown. As a rule, if a comatulid was placed at the middle of the tank, one end of which was covered over, while the other end was in sunlight, movement to the shaded end almost always was the first result. Often, however, the animal did not remain there, but moved about restlessly, even to the brightly illuminated end. In such cases it is a fair inference that the absence of suitable surface for attachment was the cause of the restlessness. More consistent results followed when direct sunlight was allowed to fall on comatulids which had been in the shade. With scarcely an exception, they moved out of the brightly lighted area. Experiments with artificial light were entirely negative, presumably because of the weakness of the stimulus, nothing better than an ordinary kerosene lamp being available. No specific differences were noted with reference to light reactions, all the species watched giving the same results. Bright sunlight thrown abruptly on a comatulid lying in shadow often produced immediate and sometimes more or less spasmodic closing of the arms over the oral surface of the disk, as though that part of the animal were most sensitive to the stimulus. In confirmation of the view that the disk is more sensitive to light than the arms is the fact that in their natural habitat the crinoids often extended the arms out into the light, while the body itself was in heavy shadow. Indeed, all along the southwestern reef, on the brightest days, they were to be seen in such a position.

RESPONSE TO HEAT.

As ice was not obtainable at Maër and it was difficult to lower the temperature of any large amount of water to any considerable degree, my only experiments with regard to the response of comatulids to temperature changes dealt with the effect of raised temperatures or, more briefly, the response to heat. The tank previously mentioned was used for these experiments, and while the results were not entirely consistent, they were sufficiently so to make them of some value. An alcohol stove placed under one end of the tank made it possible to raise the water just over the flame several degrees without appreciably affecting the temperature of the other end for nearly an hour. The sea-water brought from the reef and with which the experiments began had a temperature of 26.6° C. The area directly over the stove soon became about a degree warmer than this, while immediately above the flame it rose to 31.7°. Comatulids placed in the tank at the unheated end began at once to move towards the other end, the whole tank being uniformly illuminated. The passage into the slightly warmer water was not indicated in any way, but whenever the arms extended into the area above 30° a more or less prompt response and withdrawal followed. This was shown by all the species tested, but was most noticeable in adult *Comatula purpurea*, and consequently that species was chiefly used. If an individual were placed in the hot area, it immediately moved out, but it did not seek the coolest part of the tank. At the end of 1½ hours the water in the tank was raised to a minimum of about 29° and the comatulids were all at rest or moving very languidly. It was interesting to note, however, that transfer from this warm water to the sea-water at ordinary temperature (26.6°) acted as an immediate stimulus and locomotion was at once renewed. The reverse was also true, comatulids from the normal sea-water responding at once with active movements when dropped into the warm water. In the latter case, however, the movements very quickly ceased. As a result of these observations, it is evident that comatulids are sensitive to comparatively slight changes of temperature and that, for those living at Maër, 26° to 27° C. is about the optimum. It is not probable that the sea-water on the reefs at the Murray Islands ever gets far below that temperature, but it is often much higher, at least on the reef-flat itself. It is therefore of great interest to find that at 29° these comatulids become inactive and that they withdraw at once, if possible, from 31°. Evidently, then, a fairly uniform temperature is an essential factor in determining their distribution, and this accounts for their absence from the greater part of the reef-flat at Maër, for the water on some parts of this flat, if low tide is near mid-day, rises far above 31°. It seems probable, too, that the more uniform temperature and the absence at all times of high temperatures in the channel between Maër and Dauer are added reasons why the southwestern reef on Maër has such an abundant comatulid population. The abundant food supply in that region is thus not the only factor in the case.

RESPONSE TO OTHER STIMULI.

Mechanical stimuli met with ordinary response under normal conditions. The disk and the pinnules at the bases of the arms seem to be more sensitive to touch than either the middle or terminal part of the arms. The cirri and the whole aboral surface are slow to respond to mechanical stimulation. The response to touching the disk is a closing of the arms over it and the response to touching the oral surface of an arm is the gradual infolding of that arm. Mechanical stimulation alone, even a severe pinch of an anterior arm with forceps, seldom caused any change in the direction of locomotion. The net result of all the observations was the impression that comatulids are surprisingly callous to mechanical stimuli, and the response is never sudden or hurried.

It was particularly desirable to determine if comatulids showed a quick response to changes of salinity in the sea-water, but the results of the experiments were all negative. There was no success in securing any response to the addition of rain-water to the sea-water in the aquaria, even when the rain-water was poured directly onto the disk of the crinoid. The transfer of a comatulid from sea-water directly to rain-water met with marked response and violent movements, but as long as the water in the tank was predominantly salt, there was no visible response to the addition of rain-water. On the other hand, the increase of salts seemed to be a matter of equal indifference, but the response to a strong solution of magnesium sulphate was prompt and violent. This is the more remarkable because the reaction is so different from that shown by starfishes and ophiurans. When these echinoderms are thrown into a saturated solution of magnesium sulphate, there is a brief period of activity, but not violent, and this is followed by complete stupefaction and relaxation of the whole muscular system. Comatulids, however, respond to the stimulation of the solution so violently as to break off some or all of the arms and no evidence of subsequent relaxation was found. This peculiarity of muscular reaction in comatulids deserves much more careful study than circumstances at Maër permitted.

Alcohol poured on the disk of a crinoid in the tank brought about a very marked response, but the latent period was surprisingly long and the effect of the stimulus soon wore off. If comatulids were taken from sea-water and dropped into alcohol (or formalin), the response was immediate and consisted in the extreme contraction of the arms aborally (*i. e.*, backwards). Often this would be followed by a strong oral contraction, bringing the arms up vertically over the mouth. This again would be followed by a general relaxation followed by death and a hardening of the tissues. Specimens simply thrown into alcohol (or formalin) or placed in the fluid, mouth down, never died in a natural position, the arms being strongly contracted, usually entangled with each other and with the cirri dorsally, but sometimes shut up together over the mouth.

Owing, however, to the fact that almost without exception the first response is the contraction of the *dorsal* muscles, it is very easy to prepare perfectly expanded specimens. They are lifted from the sea-water with the cirri down and plunged abruptly into strong alcohol in a shallow flat dish, care being taken to press the disk down at once to the bottom of the dish. The contraction of the dorsal muscles causes the arms to lie out flat against the dish-bottom. The following contraction of the oral muscles is occasionally strong enough to bring the arms up over the disk and get them badly entangled, but in the very great majority of cases it is so feeble and so quickly followed by relaxation that a little manipulation of the arms, smoothing them down with the fingers and pressing out the curves, results in perfectly expanded specimens. Only in relatively few cases, and these were individuals which had been in the laboratory for some hours, was the muscular contraction great enough to break off the arm or even cause loss of cirri. These cases are, probably to be explained by the susceptibility of these comatulids to non-aerated sea-water—that is, presumably, to CO_2. It was not possible to determine positively whether CO_2 was the deleterious substance or not, but there is good reason for that belief, because the comatulids were found only on those parts of the reef where the aeration of the sea-water was very well provided by the surf. However, whether CO_2 was the factor directly responsible or not, it is beyond question that the comatulids brought to the laboratory were very susceptible to the impurity of the sea-water after a few hours in the aquaria.

If a number of specimens were left in a basin, even with a relatively large amount of sea-water, they gradually became inactive and after a time perfectly still and made no response to mechanical stimuli. That they were not dead was indicated by response to chemical stimuli (alcohol, formalin). But if left undisturbed, the arms began to break to pieces distally, the process continuing centripetally until only the basal parts of the arms were left attached to the disk. Even then response to stimuli could be induced if the specimens were placed in perfectly fresh sea-water. If, however, they were left undisturbed, fragmentation continued until even the basal parts of the arms were completely disintegrated.

There is great individual difference as to the time when amputation of the disk from the calyx takes place. It was very common to have this happen as the first step in disintegration, but in some individuals it was one of the last. Not rarely comatulids shed their disk when first taken from the sea and placed in the pail, but such specimens lived in the live-car as well, apparently, as those in which the disk and digestive system were intact. Presumably regeneration would take place under normal conditions as it does in the antedons of European seas.

SUMMARY.

1. Individual differences in the responses of crinoids to the various kinds of stimuli indicate a complex nervous mechanism and forbid any simple explanation of their reactions.
2. Important differences in the methods of locomotion and of feeding show that different groups of comatulids (genera, families, orders, etc.) may give quite different responses to identical stimuli.
3. Many comatulids, especially the large multibrachiate species, are very sluggish, and the members of the family Comasteridæ do not swim, but only creep about by use of the arms.
4. Comatulids of the families Stephanometridæ, Mariametridæ, Colobometridæ, and Antedonidæ, although ordinarily inactive, are good swimmers and do not creep as the usual method of locomotion.
5. It is doubtful if, under unchanged conditions, comatulids move about to any important extent, but it is certain that local changes can, and do, bring about considerable alteration of position and possibly real migrations.
6. Comatulids at Maër during the dry season are almost exclusively vegetable feeders, although protozoans form a small part of their nourishment. The food is not ingested as dead matter, but is unquestionably taken in as living material. Feeding is presumably accomplished by means of the ciliated furrows, and movements of the arms are certainly not essential and probably are not a very important factor.
7. All the comatulids at Maër are negatively phototactic. Brightly lighted areas are avoided and shadowed or dark places are sought.
8. The comatulids at Maër show marked susceptibility to heat and an increase of only 2 degrees produces an evident effect. Areas of markedly increased temperature are avoided.
9. The comatulids of Maër showed no response to a marked decrease in the salinity of the water and none to a slight increase of the salts. Their reaction to strong solutions of $MgSO_4$ is noticeably different from that of other echinoderms.
10. Reactions to strong alcohol or formalin are marked and well defined, and normally follow a regular sequence.
11. Reactions to impure sea-water, presumably to the CO_2 contained in it, are slow but sure. An excess of impurity soon produces inaction, followed ultimately by complete disintegration.

CONCLUSIONS.

In making my deductions from the observations made at Maër, I wish to emphasize the fact that other species of crinoids, particularly members of other families, will probably show quite different and no doubt often contradictory reactions. It is also very likely that the same species, studied in a different locality or studied at Maër, during the rainy season, would give results in some degree different from those I have secured. Undoubtedly our knowledge of the habits of crinoids as a class, or even of comatulids alone, is altogether too slight to warrant the drawing of any far-reaching conclusions. Because of this conviction it seems necessary to review Mr. A. H. Clark's paper, already referred to, and point out what seem to be the mistakes he has made apparently from basing his assertions on the study of structure rather than on the observation of living crinoids.

First, as to the crinoids being, "as a class," "probably the most strictly sessile[*] of all marine organisms: Many of them are stalked and do not move, and those forms in which the stalk is partially or entirely lost in adult life probably move but very seldom, and not at all unless under strong compulsion" (1908, Geog. Jour., London, p. 602). So far as the stalked forms are concerned there is no little reason for believing that these crinoids are rarely attached and are capable of moving about. As for the unstalked forms, I think my observations at Maër show that while it is true they are usually inactive under uniform conditions, they both can and do move, by either swimming or creeping. To consider them more "sessile" than corals, sponges, or barnacles seems to me absurd. If the reply is made that these groups all have active, free-swimming larval forms, which provide for their wide distribution, the natural answer is that comatulids also have them.

Mr. Clark says of comatulids: "Their free-swimming larval period (so far as we know) is of short duration; the larva soon sinks to the bottom and becomes fixed." The parenthetical is no doubt the saving clause here, for, excepting the European species of *Antedon*, there is not a single crinoid of which we know anything whatever about the length or habits of the free-swimming larval period.[†] Of course, Mr. Clark's opinions in the matter, based on the examination of the eggs of a number of species of comatulids (alcoholic material), may be correct, but better evidence is needed to demonstrate that crinoids are essentially different from the other classes of echinoderms in either the length or activity of their free-swimming life.

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[*] This use of the word "sessile" is admitted by the Century Dictionary, but is said to be rare. The idea is apparently not merely "sedentary," but actually "not capable of any extended movement."

[†] Elsewhere (Proc. U. S. N. M., vol. 38, p. 213; 1910) Mr. Clark, while arguing in defense of a different assumption, says that the species "of *Tropiometra* have a very wide distribution, necessitating a prolonged free-swimming stage; are we justified in saying that the larvæ of *Tropiometra* may not turn out to be plutei or something like them?" If one may argue thus with reference to *Tropiometra*, why not also with reference to the dozens of other genera concerning which we are equally ignorant?

Mr. Clark says of the young of starfishes and brittle-stars that their occurrence in numbers at the surface of the sea "indicates a power of dispersal quite unattainable by the crinoids." Here again we have a pure assumption. Starfishes and brittle-stars are more or less abundant in all regions where there are marine laboratories, and we know something about the larvæ and larval habits of a few species. Except perhaps Misaki, there is not a permanent marine laboratory in the world where more than a single species of crinoid is available for study, and comatulids are common only in regions which have as yet been hardly touched by the student of echinoderms. It is unreasonable to base an argument on what we do *not* know.

Further on in his paper (p. 603), Mr. Clark contrasts crinoids, as "practically sessile" organisms, with sea-urchins, starfishes, and brittle-stars. Judging wholly from my observations at Maër, where more than 20 species of crinoids, 20 of starfishes, 50 of brittle-stars, a dozen of sea-urchins, and 40 of holothurians were collected on the reefs, I should say that echini are the most sedentary ("sessile") of the five classes. Certainly nearly all echini, most holothurians, and many starfishes are quite as inactive as the comatulids. Many echini and some holothurians live in holes and crevices in rock which are apparently prisons and from which they do not, and sometimes certainly can not, move. I have never found a comatulid so situated. In this connection it is appropriate to quote a paragraph from a letter written by Dr. L. E. Griffin, formerly of the Bureau of Science, Manila: "I saw in 'Science' that you discovered crinoids swimming at Maër. One I sent you from Culion was a very active swimmer and lived among the eel-grass. We have often seen them swimming in the P. I."

In reference to the food of crinoids, Mr. Clark says (pp. 603–604) that "at or near the surface a crinoid must depend upon" small pelagic organisms "which swim within reach of its pinnules or which it may intercept with the slow motion of its arms." These words seem to indicate that Mr. Clark looks upon the food as being captured by the crinoid, whereas it appears to be simply a matter of passing the sea-water, actually swarming with organisms too minute to be individually captured, through the ciliated furrows to the mouth. Mr. Clark goes on to say that "in deeper water," the crinoid would get, in addition to this food supply, "all the carcasses" of the organisms which die in the water above it. And he concludes: "The intensity of this rain of food increases, of course, proportionately with the depth, so that the deeper a crinoid lives the greater is the available food-supply; consequently, the better nourished is the individual and the greater is its size." (In justice to Mr. Clark it should be added that he sets 600 fathoms as a limit beyond which this rainfall of dead organisms would cease to be available for the crinoids.)

The two questions which arise in connection with this original theory are: first, is there such a rainfall of carcasses? and, second, if there were, would the crinoids use it for food? In regard to the existence of such a "rainfall of carcasses," there is room for some skepticism. Pelagic microörganisms appear to live (except when overtaken by some sudden catastrophe covering a wide area of sea) until eaten by some larger organism. There is little evidence that they die of either disease or old age. The material collected by tow-nets, both at the surface and at more or less considerable distances below it, usually contains a surprisingly small amount of dead material (excluding of course dust, sand, chaff, etc., from the shore).

Mr. Clark recognizes the necessity of some special cause for the slaughter of the microörganisms and finds it in the decreasing of the salinity of the sea-water by supplies of fresh water from melting ice, flooded streams, and torrential rains. With regard to melting ice, he offers the following illustration: "The west coast of Greenland abounds in fjords which are continually giving off fresh-water ice, which floats off melting as it goes, thereby killing millions of small organisms which are unable to endure a great change in the salinity of the medium they inhabit." If the fresh-water ice is "continually" given off, it is hard to see how the salinity of the sea thereabouts can undergo any "great change." Moreover, how about the long Arctic winter, when there is practically no ice movement out of the fjords? The intermittent and uncertain appearance of floods and torrential rains seems to render them very improbable factors in the wholesale death of the plankton, although it is quite possible that occasionally they may play the part that Mr. Clark demands of them.

But even granting the "rainfall of carcasses," there is no evidence that it would serve as food for the comatulids among which it fell. Judging from the observations at Maër, comatulids live and thrive only where conditions permit a very rich vegetable plankton to swarm in the water. Where such a plankton exists, no amount of animal matter added to it, either dead or alive, will greatly affect the comatulid's food. Moreover, crinoids, at least comatulids, do not live lying exposed, oral side up, on the open bottom of the sea, but are concealed under rocks with the oral side down, where a rainfall of carcasses or of other food would scarcely reach them at all. Or they live among corals and sponges, so protected that very little of such a supposed rainfall would ever reach them.

Of course, the observations made at Maër are exceedingly few and deal with a small number of species, in a very limited area, but they are almost the only *facts* that have yet been published on the subject. On *a priori* grounds, deep-sea crinoids living below the limit of vegetable life must be animal feeders, but as yet we know nothing as to the composition of the food, and there is no reason to suppose it consists of "carcasses."

Mr. Clark says (p. 606) that very large species of "Comasteridæ occur abundantly in very shallow water, often just below the low-tide mark" in the tropics. This is apparently true for Maër, though it is not clear what Mr. Clark would call "very large." But when he says that the individuals "decrease in size with depth," doubt may well be felt. Of course, when a depth sufficient to diminish the amount of vegetable plankton is reached comatulids very possibly become fewer and smaller. No crinoids were taken at Maër at a depth sufficient to throw any light on this point. It is certainly true at Maër, as Mr. Clark goes on to say, that "the beaches and rocky shores warm up, to be covered again at high tide with comparatively cool water full of organisms," but when he adds the words "unable to stand a great change of temperature," we may well ask for evidence. On the reef flats at Maër we found that many organisms living in the area where at low tide the water became heated were able to thrive within wide limits of temperature. Moreover, as the cold water of the incoming tide comes over the flat, it is not appreciably raised in temperature, but brings down to its own degree the water, rocks, and sand which have been heated. There was never the least evidence of the destruction of pelagic life on the reef flat due to heat. But even granting that such a destruction does occur, why should Mr. Clark say it would be "swept back into the sea, to fall just beyond the low-tide mark?" Would it not be just as probably washed up on the beach, dropped on the reef-flat, or carried far out to sea by the receding tide, as deposited just below low-tide mark?

In conclusion, on this subject of the food of crinoids, the legitimate criticism of Mr. Clark's views may be summed up in this way: While there need be no quarrel with his assumption that a big food-supply will give rise to big crinoids, as there certainly is such a factor in the growth of some species of starfish, it must not be forgotten that it is after all only an assumption. When to this he adds the assumption that animal food, especially in the form of a hypothetical "rainfall of carcasses," is the fundamental factor in accounting for the distribution of big crinoids, we may well become exceedingly skeptical, since the evidence obtained at Maër shows that the comatulids are vegetable feeders, and live in such positions that no "rainfall" of food could readily reach them. Finally, the assumptions, by which he attempts to account for the existence of the hypothetical "rainfall of carcasses" in the various regions where the size of the crinoids seems to require it, appear to be as dubious as they are ingenious. While fully recognizing how limited our knowledge of crinoids is, we are obliged to maintain that there are few facts known which give any support to Mr. Clark's conclusions.

In his discussion of the colors of crinoids, Mr. Clark has a much better basis of fact, but here too he makes certain assumptions that can not be accepted. He says (p. 606) that yellow is "the colour of small specimens and of pentacrinoid young of comatulids, with very few exceptions." At Maër, a considerable number of small crinoids were collected, the young of *Comatula purpurea* and of *Comanthus annulatum*, chiefly. Not one of these was yellow or even light-colored. They appeared to be mostly black, but in view of Mr. Clark's statement that black is a very rare color among comatulids, they may perhaps be called dark olive or dark brown. He adds that "red is the color of all young which are not yellow." One or two young which were red were found, but they were very unusual. He goes on: "The black factor in coloration is merely the result of age and nothing more; all full-grown crinoids become dusky," except certain yellow species. It must be said that at Maër many obviously very young comatulids were so dark that they were apparently black, while many full-grown specimens were brilliant green or red, with very little or no black.

Concluding his remarks on color, Mr. Clark claims (p. 607) that his analysis of the coloration of crinoids "explains the wide range of hues found in these animals; they appear to be merely the result of light, which introduces a blue factor on a pigment primarily yellow, more rarely red, plus the effect of the age factor, black. Not only the crinoids but all the echinoderms appear to obey this law." It is regrettable that the problem of the coloration of echinoderms is not so easy of solution and not so nearly solved as this naïve remark of Mr. Clark implies. It is not difficult to think of numerous cases to which his theory would not apply in any way whatever, and while that theory may prove of value ultimately in helping us to understand the coloration of certain groups of crinoids, the claim that it is a "law" is somewhat premature, while the statement that it appears to be applicable to all echinoderms is simply preposterous.

V.

THE PLUTEUS OF LAGANUM SP.

BY GRACE MEDES.

Twenty-two text-figures.

THE PLUTEUS OF LAGANUM SP.

By Grace Medes.

The *Laganum* plutei used for this study were obtained by Dr. D. H. Tennent, November 1913, at Badu Island, while with the expedition sent out to Torres Straits by the Department of Marine Biology of the Carnegie Institution of Washington. I am indebted to him, not only for the material, but for constant assistance throughout the work.

The plutei preserved by him are of two ages, 29 and 55 hours respectively. The former were fixed in Flemming's stronger chromo-aceto-osmic mixture for 6 hours and preserved in alcohol; the latter, which were designed solely for study of the skeletal structures, were killed in fresh water and preserved at once in alkaline alcohol.

The 29-hour specimens were used entirely for study of the tissues. They were embedded in paraffin, sectioned, and the sections subsequently stained by Heidenhain's iron-hematoxylin method. The 55-hour specimens, which were too opaque for study in the whole mount, were gradually transferred to water, left 4 hours in a 5 per cent aqueous solution of potassium hydroxide, and after washing an hour, were dehydrated and mounted in balsam. This method, which proved highly satisfactory for preparing these skeletons for microscopic study, was adapted from a process described by Mr. L. M. Peace (5), who recommends its employment for clearing opaque plant tissues. The chloral hydrate solution suggested in the same article could not be used, as it is so strong a corrosive that specimens treated by it became too fragile for further manipulation. The potassium hydroxide removes just enough of the softer tissues to render the specimen transparent, at the same time leaving it sufficiently hard for subsequent washing and dehydration. The latter process was always done on the slide, to which the specimen was made to adhere by allowing it to dry slightly while in the lower grades of alcohol.

For detailed study of the more minute structures, such as the enterocœles, it was found necessary to use reconstructions, which were accordingly made from both longitudinal and transverse sections. In addition to those of the whole animal, separate ones of the lumen of the hydrocœle and of its lobes were also modeled. For making the reconstructions Born's method was employed, with plates of beeswax brought to the proper consistency by mixing with Venice turpentine.

All of the drawings were made from camera-lucida outlines taken with Zeiss objective $\frac{1}{8}$ and oculars 4 and 6. Figures 4 to 15 were again enlarged with camera drawings magnifying to twice the number of diameters. Figures 2 to 15 have been taken from the 55-hour specimens, all others from the 29.

INTERNAL STRUCTURE.

The body of the 29-hour plutei of *Laganum* is ovoid in shape, in some cases almost spherical, with a flattened or slightly concave anterior surface (fig. 1). Two larval arms grow out from a position somewhat dorsal to the center of the antero-lateral regions. In the 55-hour specimens, the body has elongated slightly and the posterior end has become somewhat pointed. In the earlier stage the arms extend outward at an angle of about 60° from the body, while in the older form they are more slender and reach upward nearly parallel to each other.

An opening to the exterior lies in the center or slightly to the right of the center of the flattened anterior surface. It may be seen readily in the whole mount, but no other opening can be observed. The animal itself is exceedingly opaque, so that no study of the internal organs could be made except in specimens especially fixed and bleached for observance of the skeletal structures. Unfortunately, in this detailed treatment the tissues were so largely destroyed that study of them was impossible.

Among the specimens studied, about fifty in all, I have found three which show interesting variation in structure—two with 3 larval arms, and one with 5. In the former case the third larval arm arises from the center of the dorsal margin of the anterior surface, while in the latter instance there are, in addition to this one, 2 on each antero-lateral margin, one immediately dorsal to the other. All the arms are of about the same size, and in other respects the pluteus seems to be normal, but since these three specimens were found among those preserved especially for the skeletal structure, no further study of the internal anatomy could be made. The possibility exists, of course, that they represent the normal development of a later stage, but this scarcely seems probable in view of the complex condition already attained by the remaining portion of the larval skeleton and the advanced stage of development of the echinoid rudiment and permanent skeletal structures.

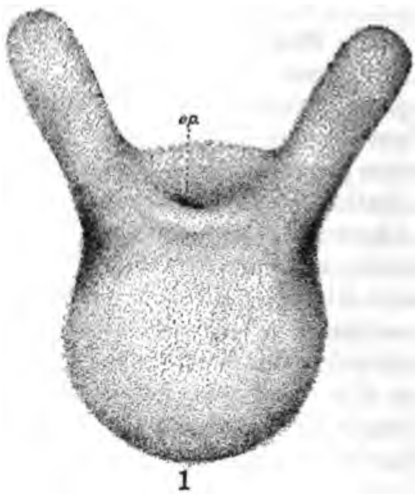


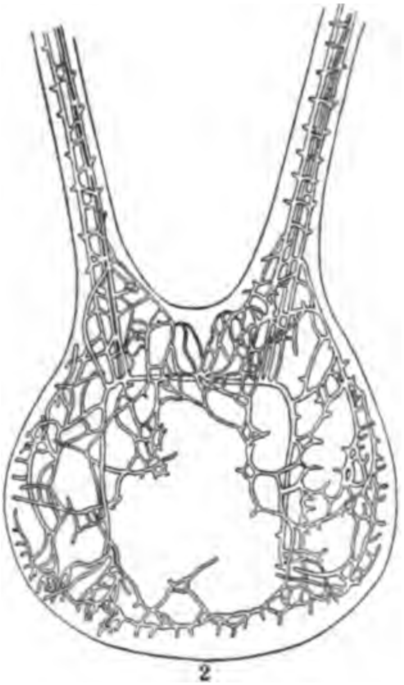
Fig. 1.—*Laganum* pluteus, 29 hours, viewed ventrally and somewhat anteriorly. *op.*, opening into amniotic cavity. × 130.

INTERNAL ANATOMY.

THE LARVAL SKELETON.

The larval skeleton is primarily a paired structure, each half of which supports one side of the pluteus. Each portion consists essentially of three parts: a transverse rod lying across the anterior end of the animal; its antero-posterior prolongation in the lateral wall of the pluteus; and a latticed rod supporting the corresponding larval arm.

The transverse rods, after crossing the body in about the anterior third, bend nearly at right angles, and pass toward the posterior end of the pluteus. During their course they send out toward the periphery many irregular branches which anastomose repeatedly and gradually form a close network surrounding the animal on all but its ventral surface. The skeletal structure of this ventral region consists mainly of a branch from each primary lateral rod, which sweeps around ventrally and may even cross that of the opposite side in the median line (fig. 3). These give out similar anastomosing branches, which, however, never attain the high degree of complexity characteristic of the skeleton in the dorsal region. The network becomes finer just beneath the ectoderm, into which it projects innumerable short, spine-like processes. The skeletal supports of the arms are each made up of 3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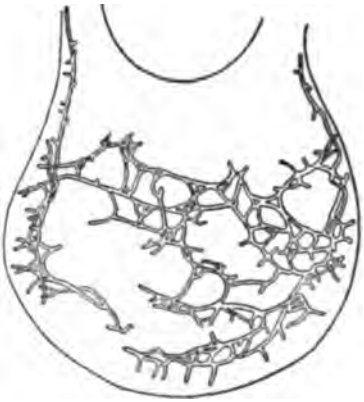
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Fig. 2.—Dorsal portion of larval skeleton of *Laganum*, 55 hours, drawn from ventral side. × 130.
Fig. 3.—Ventral portion of skeleton of same specimen as fig. 2, also from ventral side. × 130.

simpe rods united at short intervals by more or less irregular connecting bars (fig. 2). From the nodes short spines project toward the periphery. Near the base of the arm these spine-like processes become longer and they themselves give out branches which unite with one another, so that an irregular lattice-work is formed continuous with that in the body of the pluteus.

In the pluteus possessing 3 larval arms, the transverse rods are shorter and are met by a third rod to which those supporting this arm are attached. All of these bend downward at their ends, giving off long sweeping branches directed posteriorly. In the larva with 5 arms there is also a corresponding number of transverse rods.

THE PERMANENT SKELETON.

PLATES.

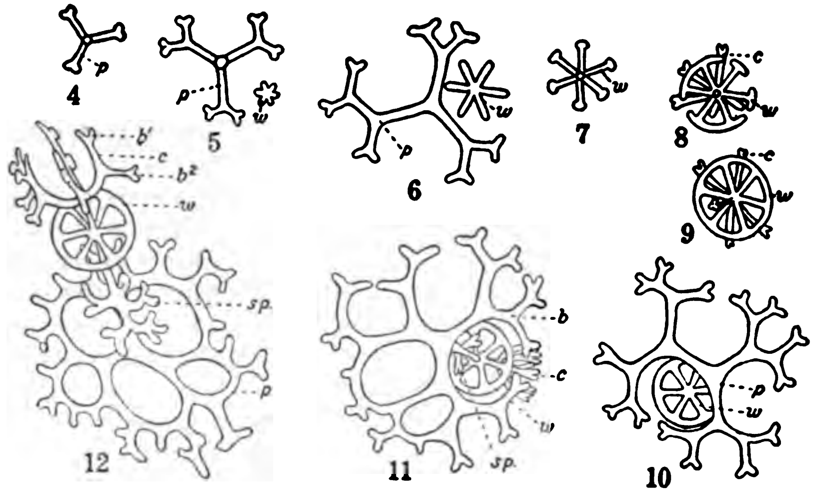
Although the specimens are all of the same age, a considerable variation exists among them as to degree of development of the permanent plates, so that I have been able to obtain a series showing more fully the early development of these and of the simultaneously developing spines than of any of the other structures (figs. 4–16).

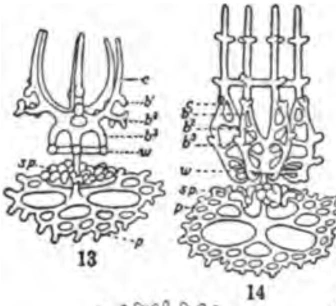
In those specimens showing the most advanced stage of development, the permanent skeleton consists of a circle of 5 plates surrounding the region where the mouth is to form, one of which lies anteriorly, 2 laterally, and 2 posteriorly (fig. 16). Outside of these is a circle of 10; 2 lie back of the anterior, 1 back of each lateral, and 3 are clustered behind each of the 2 posterior plates. As a consequence the mouth anlage has an eccentric position, somewhat to the anterior of the resulting skeletal structure. The plates are all similar and are those to which the first spines are attached. Many of the specimens are in this stage and possess 15 spines and plates. But new ones are constantly developing which crowd the surrounding area as well as push in among those of the first two rows, so that later no definite arrangement can be determined.

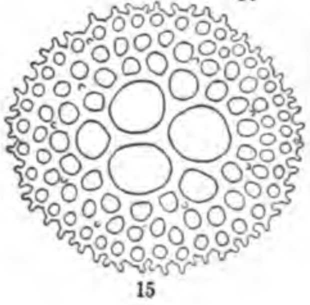
Each plate commences as a triradiate spicule (fig. 4), the radii lying in the same plane and at angles of 120° to one another. Afterwards a fourth branch arises from the center and pushes outward, and it is to this that the spine later becomes attached. Figures 4 to 7 and 10 to 14 give a series of these developing plates. The 3 primary radii soon divide, each time at about the same angle (figs. 5, 6, 10), so that by repeated division 3 hexagonal spaces are inclosed (figs. 10, 14). By the continued pushing out and rebranching of the radii a plate like that shown in figure 15 is formed.

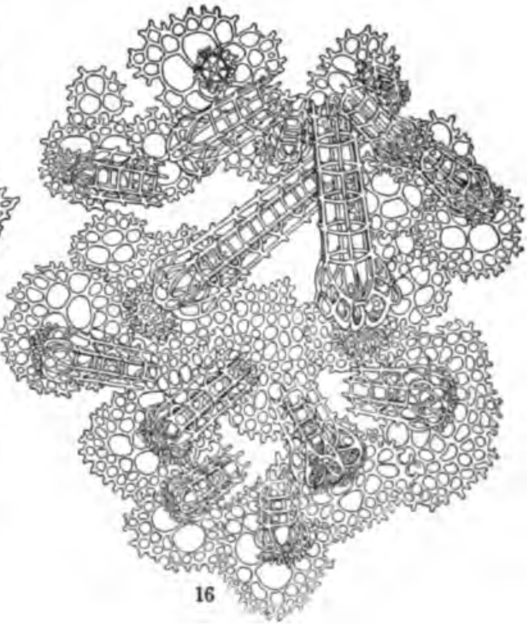
SPINES.

Early in the development of the structure described above, a second spicule, with 6 rays instead of 3, may be observed lying near each plate and external to it (figs. 5 and 6). Each ray of this new structure soon









Figs. 4 to 15.—Series showing development of plates and spines of the permanent skeleton of *Laganum*. Figs. 4, 5, 12 to 15 viewed from ventral surface. 6 to 11, from dorsal surface. b^1, b^2, b^3, branches from each of the six primary rays, which by uniting with one another and with the wheel-like structure at their exterior ends, form 6 radiating plates in the base of the spines; *c*, 6 branches of the primary rods which form the cup-like basal portion of the spine; *p*, plate; *ps*, portion forming small secondary plate which lies between the primary one and the spine; *w*, portion forming wheel-like base of the spine. Figs. 4-10, ×466. Figs. 13-15, ×350.

Fig. 16.—Permanent plates and spines viewed from the oral surface, showing their characteristic arrangement around the anlage of the adult mouth, *m*. *a. p.*, adult plate; *a.s.*, adult spine. ×265.

develops a knob-like tip (fig. 7) which spreads laterally until it meets and fuses with those of the adjoining rays. Gradually a wheel-like structure is formed (fig. 9). Figure 8 represents one at a slightly earlier stage.

From the center of this structure there has already grown out in each direction a calcareous rod in the position of an axle (figs. 7, 8). The one which points internally sends out at its tip a mass of irregular branches which lie in a plane parallel to the wheel (figs. 8, 9, 11, *sp.*), and which unite to form a small plate below the spine (figs. 12, 13, 14, *sp.*). The rod that has grown out from the center of the original plate now fuses with the base of this structure (fig. 13), so that the calcareous part of the spine is united with the permanent plate of the developing embryo.

The rod which pushes out externally from the wheel divides into 6 branches that grow up into a cup-shaped structure (fig. 11); each of these now sends out externally 3 branches, the lowest of which bends downward and joins the wheel at the end of a spoke (fig. 13, b_3). The uppermost of the three grows downward to meet the second and it in turn sends down a branch to meet the third. Meanwhile each of the original 6 rods has begun to elongate and to send out branches right and left at regular intervals, which meet those of the adjoining rods. This forms the lattice-like skeletal structure in the developing spine (fig. 16).

THE AMNIOTIC CAVITY.

In the younger of the two stages studied, the embryo forms but a small part of the pluteus, while the amniotic cavity, crowded with the developing spines, occupies the greater portion. Just how this cavity has developed it is impossible to state, since I possess no stages young enough to show it in the process of formation, but it seems possible that it has grown in from the ventral surface by a process of involution, gradually pushing back the gut which may already have lost its connections with the exterior. Figure 20 shows a median sagittal section of such a pluteus. The external opening leads directly into the amniotic cavity, which at this stage is filled with about 15 spines in various stages of development. This opening apparently does not close over, since it is still present in the 55-hour stage when the spines are now pressing closely against the exterior wall of the amniotic cavity. There is no indication of the formation of a mouth.

In correlation with the unusual position of this cavity, the echinoid rudiment, instead of occupying one side of the pluteus as in other described forms, now becomes pressed back to a central position with the amniotic cavity surrounding all but its aboral surface, so that the dorsal surface of the pluteus forms the aboral surface of the adult. The opposite wall of the embryo, separating it from the amniotic cavity, becomes the oral region, and in it the permanent plates develop, encircling a region slightly anterior to the center, beneath which lies the ring of the hydrocœle. Here, then, the adult mouth is evidently to form.

The wall of the amniotic cavity is composed of 2 layers of tissue which are continuous with each other around the external opening. They consist of an inner layer of large irregular cells, and an outer epithelium of cylindrical cells with darkly staining nuclei, usually situated well back toward the base of the cell. In the inner layer the cytoplasm is clear, and takes the form of a loose, irregular meshwork; in the outer it is opaque and is crowded with pigment granules exterior to the row of nuclei. Occasionally, however, large areas may be found in the outer layer, within which the cytoplasm contains many irregular vacuoles, indicating that possibly the wall of the amniotic cavity is beginning to break down.

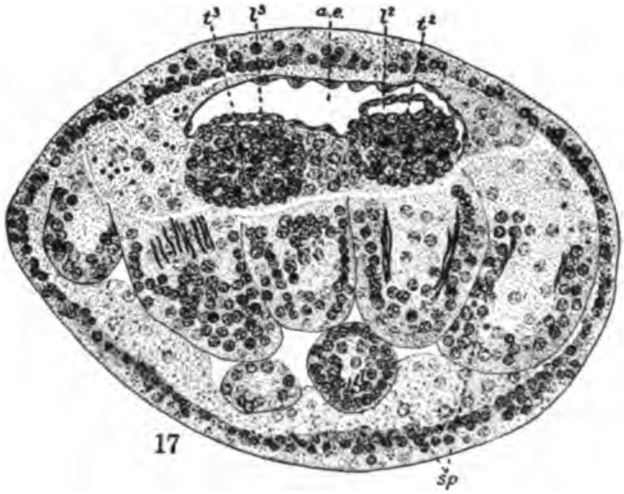


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FIG. 17.—Transverse section through anterior part of body, showing two anterior primary tentacles. *a.e.*, anterior enterocœle; l^2, l^3, lumen of lobes 2, 3, of hydrocœle; *sp*, spine; t^2, t^3, tentacles 2, 3. × 233.

Histologically, the spines also are composed of 2 layers of tissue. The inner central one forms a core in which the cytoplasm possesses a large irregular meshwork. In the outer the cytoplasm is denser and crowded with pigment granules, and the nuclei stain more heavily with the hematoxylin. Between these two layers lie well-developed longitudinal bands of muscle. Within the spines were originally the skeletal supports described above, which have been destroyed in these specimens by the fixing fluid.

THE ENTEROCŒLES.

Within the embryo, transformation from larva to adult is already beginning to take place. The gut has lost its opening to the exterior, the left posterior enterocœle is definitely constricted from the anterior, and the hydrocœle with its 5 primary tentacles is already in an advanced stage of development.

The gut is markedly compressed dorso-ventrally. There is no definite division into œsophagus, stomach, and intestine, although its much greater size in the central region indicates the probable location of the stomach. At the anterior end the tube tapers more gradually than at the posterior, where it retains a tendency to curve somewhat toward the ventral surface of the embryo. The gut is lined with a single layer of cylindrical cells with clear cytoplasm and centrally located nuclei. The lumen is entirely closed and there is no indication of communication with the exterior.

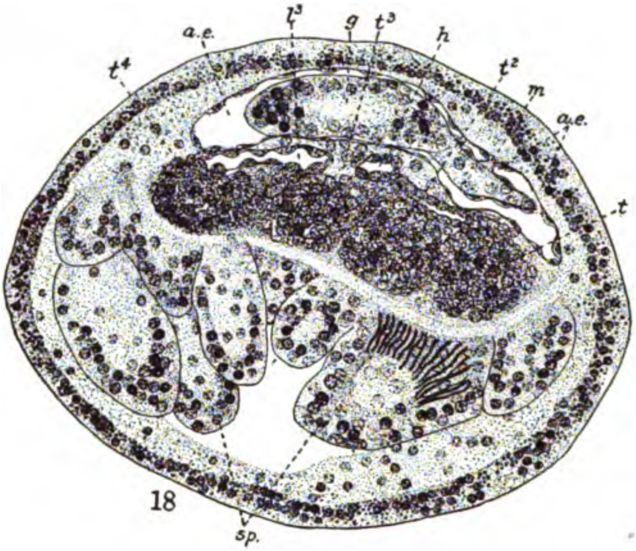

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Fig. 18.—Transverse section taken somewhat posterior to that represented in fig. 17, showing first and fourth tentacles cut through their anterior part, and lobes two and three through their posterior. *a.e.*, anterior enterocœle; *g*, gut; *h*, hydrocœle; l^3, lumen of lobe 3 of hydrocœle; *m*, mesentery-like strand of tissue connecting the stomach with the wall of the embryo; *sp.*, spine; t^1, t^2. t^3, t^4, tentacles 1, 2, 3, 4. × 233.

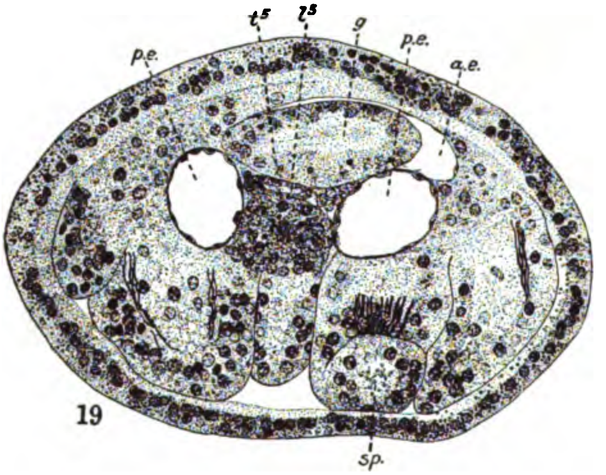

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Fig. 19.—Transverse section through posterior part of embryo. *a.e.*, anterior enterocœle; *g*, gut; l^5, lumen of lobe 5 of hydrocœle; *p.e.*, posterior enterocœle; *sp.*, spine; t^5, tentacle 5.

Anterior to the stomach, and bending down over it, lies the undivided anterior enterocœle. It is composed of an exceedingly thin layer of cells which lies flatly pressed against the adjacent tissues, except where the large, darkly stained nuclei bulge out prominently into its cavity. The lumen is largest at the right and left sides of the gut, while in the region of the mid-line, dorsal and ventral to the stomach, the enterocœle is so compressed that the walls often lie in actual contact. In many of the specimens, moreover, it does not completely surround the gut, but is interrupted by a strand of cells connecting the stomach with the aboral wall of the embryo. This commences slightly to the left of the midline at the anterior end of the stomach, and gradually curves to the left side as it approaches the posterior. That this mesentery-like structure is not a permanent one is shown by the fact that in many of the specimens, especially those showing a slightly more advanced stage of development, it is entirely lacking and the lumens of the right and left lobes of the enterocœle communicate freely around the dorsal side of the stomach. Figure 20 shows a specimen in which the tissue is especially well developed.

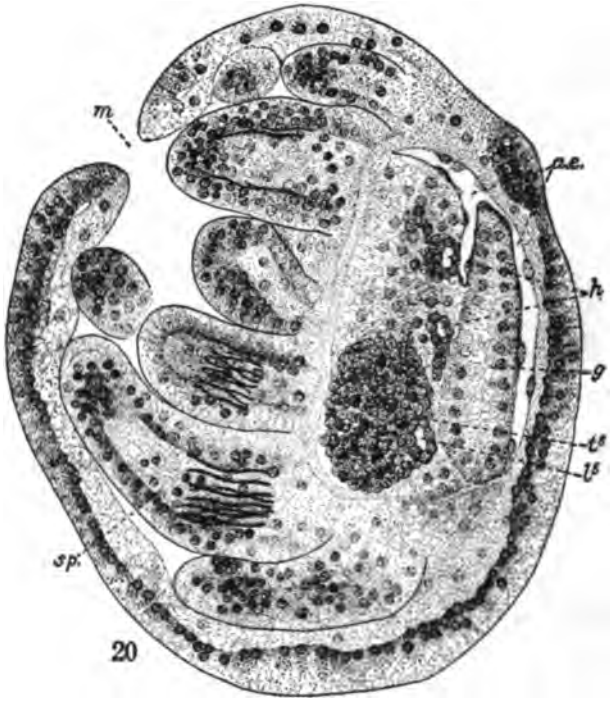

Fig. 20.—Median sagittal section. *a.e.*, anterior enterocœle; *g*, gut; *h*, hydrocœle; l^5, lumen of lobe 5 of hydrocœle; *m*, opening into amniotic cavity: *sp.*, spine; t^5, tentacle 5. × 233.

Considering the fact that the enterocœle is as yet undivided, the hydrocœle has attained a remarkably advanced stage of development. The ring is well formed, and in some cases closed. It occupies a position ventral to the anterior portion of the gut, in the mid line. It is composed of small, cuboidal cells with dense, rather opaque cytoplasm and conspicuous nuclei, and contains a small but definite lumen. There are 5 prominent lobes which have already differentiated into the well-developed primary tentacles. In this stage these are spherical or slightly elongated structures which take up the stain and retain it much more tenaciously than do any of the other tissues. The small, round lumen lies well to the dorsal side, where the wall is composed of a single layer of cells.

The fifth lobe of the hydrocœle is the most posterior, and lies directed downward opposite the posterior end of the stomach (fig. 20). The second and third are the most anterior, and lie side by side near the anterior termination of the gut. They are directed anteriorly and somewhat laterally. Figure 17 shows a transverse section passing through the two corresponding tentacles, and consequently gives a slightly oblique section of the lumen. The fourth lies on the right side of the embryo between lobes 3 and 5, and is directed laterally and somewhat posteriorly. The first is situated opposite it on the left side of the median line. Figure 18 shows a transverse section through the embryo at such a level as to cut through the anterior portion of the first and fourth tentacles and the posterior part of the second and third. The pore canal is given off from the hydrocœle ring between lobes 1 and 2. It passes dorsally toward the wall of the stomach, where it turns to the left and, circling around that organ, takes a course at first directed posteriorly and then dorsally until it reaches the aboral wall of the embryo, where it opens upon the exterior. The pore canal is

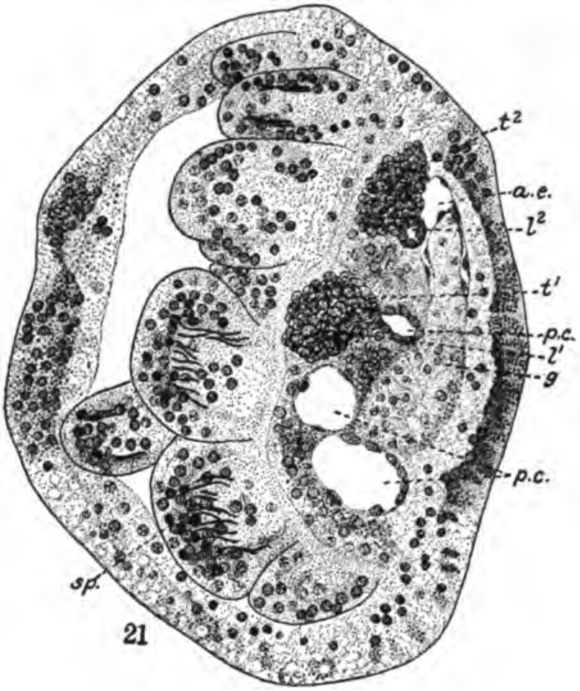

FIG. 21.—Sagittal section to left of embryo, through two vesicles of left posterior enterocœle. Pore canal is seen near first primary tentacle, just as it is given off from the ring of the hydrocœle. *a.e.*, anterior enterocœle; *g*, gut; *l^1*, *l^2*, lumen of lobes 1, 2 of the hydrocœle; *p.c.*, pore canal; *p.e.*, left posterior enterocœle; *sp.*, spine; *t^1*, *t^2*, tentacles 1, 2. × 233.

evidently just in the process of formation at this stage, since in many of the specimens it can be traced only a short distance from the hydrocœle ring and no external opening can be found. In some, however, it may easily be followed throughout its entire length. No structure corresponding to an ampulla is present. Figure 22 represents a sagittal section taken through the left side of an embryo showing the external termination of the pore-canal. In figure 21 its connection with the hydrocœle near the first lobe is represented.

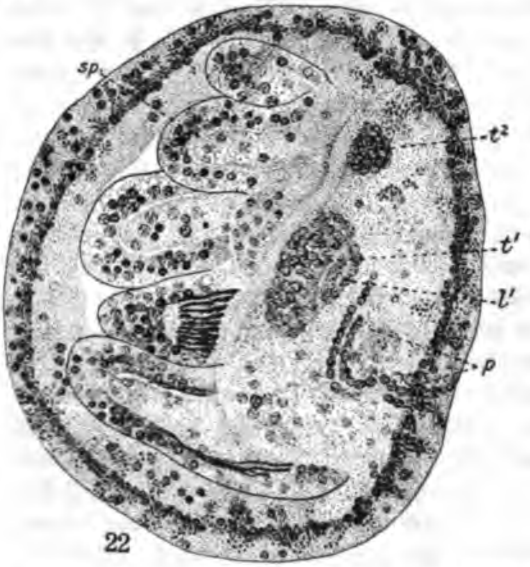

Fig. 22.—Sagittal section through left side of embryo, showing exterior opening of pore canal. l^1, lumen of lobe 1 of the hydrocœle; *p*, pore canal; *sp*, spine; t^1, t^2, tentacles 1, 2. × 233.

Toward the posterior end of the embryo, and on each side of the fifth primary tentacle, lies a spherical vesicle with a thin wall resembling that of the anterior enterocœle. These two vesicles probably represent the left posterior enterocœle. Only in one instance could I find any connection between them—a very narrow canal which circles around on the dorsal side of the tentacle. In all the other instances the two vesicles are entirely distinct. In many specimens one of the vesicles has divided, so that a smaller one lies just anterior to the first. Sometimes this division has occurred on the right side, at other times on the left, and in a number of cases the process of constriction seems to be just taking place. In one specimen 2 vesicles are present on the left side and 3 on the right.

DISCUSSION.

The development of *Laganum*, while conforming essentially with the general method of growth of other echinoderms, possesses many interesting differences as to details, as may be seen even in an investigation necessarily as incomplete as is afforded by a study of one period of its life-history.

RATE OF GROWTH.

One of the most unusual features of the pluteus under consideration is its rapid rate of development as compared with that of other described forms. In *Echinocardium cordatum* (MacBride 4) the first trace of the "Echinus rudiment"—that is, the lobe of the enterocœle representing the rudiment of the water-vascular system and the invagination of the ectoderm subsequently forming the amniotic cavity—occurs when the animal is 9 days old. By the tenth to the twelfth day the "hydrocœle has become marked into incipient lobes which are the rudiments of the radial water-vascular canals and of the primary tube-feet of the adult," and at 18 to 22 days the formation of adult spines commences. *Echinus esculentus* (MacBride 3) requires normally 16 to 17 days to attain a stage of development corresponding to that of *Echinocardium cordatum* at 9, while the spines of the adult do not appear until the thirty-third to the thirty-sixth day. In *Echinocyamus pucillus* (Théel 7) the primary tentacles are well formed at 12 days, and shortly afterward the calcareous plates and skeletons of the spines are laid down. In *Toxopneustes* (Tennent, unpublished notes) while the early development is comparatively rapid, the "Echinoid rudiment" is not well formed until about the twenty-fifth day. In *Laganum*, at 29 hours, the hydrocœle ring is already closing and its lobes have differentiated into the primary tentacles. The amniotic cavity occupies a large part of the pluteus and is crowded with well-developed spines. At 55 hours the entire oral surface is covered with permanent plates bearing the skeleton of the spines, while the larval skeleton has attained a stage of wonderful complexity. Other forms of approximately the same age are in the early stages of larval development. *Echinocardium cordatum* (MacBride 4) at 30 hours has merely completed gastrulation, while *Echinus esculentus* (MacBride 3) at 1 day has just become a fully formed and free-swimming blastula. *Toxopneustes* (Tennent 6) reaches the pluteus stage at 24 hours.

FORMATION OF THE AMNIOTIC CAVITY.

The amniotic cavity, as stated above, is already present in the earliest stage of my material, so that necessarily no positive statement as to its method of formation can be made. Although the possibility of a lateral invagination and a secondary shifting is not absolutely excluded, the unusual position it occupies and the position of its external opening permit the supposition that it may have developed in a manner unlike that described for other related forms. Goto (2), in discussing *Asterias pallida*, has maintained that "the plane of bilateral symmetry of the adult coincides with that of the larva, and that the oral side of the former is the anterior side of the latter and the aboral side the posterior." This is almost the case in *Laganum*, where the anlage of the mouth of the adult is located in the anterior part of the ventral surface of the larva. In *Asterias pallida* this condition comes about by a gradual growth of the organs of the left side towards the median line. If the amniotic cavity of *Laganum* is formed in this manner it must be accomplished at an exceedingly early period, since in the specimens under observation no trace of any such previous condition remains. Moreover, if the formation of the amniotic cavity has been accomplished by a separate invagination from the left side, the subsequent opening of the mouth into it presents an additional vexatious question.

THE ENTEROCŒLES.

The median position of the hydrocœle is also in striking contrast with the location of the corresponding structure in other echinoderms, in all of which it is described as lying on the left side. Since in this stage of *Laganum* all connection of the hydrocœle with the anterior enterocœle has been lost and no direct evidence remains as to its mode of development, it seems unwarranted to ascribe to it an origin differing from that of other known forms. The structures that I have called the posterior enterocœle are still more unusual, not only on account of their different position, but also because of their striking dissimilarity in form from those of other plutei. They lie as two entirely separate spherical vesicles, ventral to the stomach on either side of the posterior lobe of the hydrocœle. That they have had a common origin seems highly probable from their close resemblance to each other as well as from the fact that they stand in similar relation to the spines on the oral surface of the embryo. In many instances these spines, passing directly through the wall intervening between the embryo and the amniotic cavity, lie with their tissues in direct contact with the lumen of the vesicles. The same condition occurs in forms where one of the vesicles has divided, and from the smaller anterior one other spines seem to emerge.

That no structures are present corresponding to the right hydrocœle and right posterior entercœle is rather remarkable considering the advanced stage of development of those of the opposite side. The undivided condition of the anterior enterocœle is less unusual, though not of common occurrence in other closely related forms. According to Bury (1), Echinoids and Ophiuroids possess two separate enterocœles which lie at the sides of the œsophagus. Moreover, among the Asteroids the same condition obtains in the Bipinnaria. However, in the older stages of these forms a secondary fusing often occurs, especially in the region of the preoral lobe, so that a common cavity comes to be present.

In *Asterina* (Bury, 1), while the anterior enterocœle is essentially a double structure, there are three communications between them—a ventral just below the hydrocœle and two dorsal, one just above the hydrocœle and a second behind the pore. In *Laganum*, although the body of the embryo is compressed dorso-ventrally and the lumen of the cavity in that region is consequently very narrow, there seems to be no separation of the right and left portions into distinct lobes.

BILATERAL SYMMETRY.

It is evident that in *Laganum* there exists a bilateral symmetry not characteristic of other forms of echinoderm larvæ at a corresponding stage of development. The cavities of the anterior enterocœle at each side of the gut are usually of about equal size and extend approximately the same distance towards the posterior end. The ring of the hydrocœle lies immediately in front of the centrally located gut, and its lobes have a perfect bilateral symmetry with regard to the median plane of the animal. On each side of the posterior primary tentacle lies one of the vesicles which together represent the posterior enterocœle. The only interruption of the bilateral symmetry is caused by the pore canal which, arising from the left side of the hydrocœle ring and circling around the gut, opens to the exterior, well to the left side of the pluteus.

Whether this symmetry, which has not been described for so late a stage of the echinoderm, is a primary or a secondary development could of course be definitely determined only by a study of earlier stages. But, however this condition arises, it is evident that we have here a form unusual not only in regard to this characteristic, but also in respect to other fundamental properties, such as the rapidity of early growth, the great complexity of the larval skeleton, the formation of the amniotic cavity from a central invagination, the entire absence of right posterior enterocœle and hydrocœle, and the complete constriction of the left posterior enterocœle into two separate vesicles.

Bryn Mawr College, *January 8, 1915.*

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VI.

THE PERMEABILITY OF CELLS FOR ACIDS.

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THE PERMEABILITY OF CELLS FOR ACIDS.[1]

BY E. NEWTON HARVEY.

The results of researches on the permeability of cells for alkalies, using the color change of an indicator, neutral red, within the cell as a convenient method of detecting penetration of the alkali, were published[2] by the present author in 1911. Bethe[3] and also Warburg[4] had used the same method for certain of the alkalies, although I was unaware of their experiments at the time. Bethe likewise found that if medusæ (Rhyzostoma) are stained in neutral red, they become orange red in color and if HCl is then added to the sea-water the orange red does not change to bright red until the tissues are killed. In the meantime, loss of irritability on the part of the muscles has occurred while the neutral red dye is still orange red in color. In my experience neutral red has always been taken up by cells in a bright-red condition, so that acid, if it entered the cell, would produce no further marked color change. I have found it likewise impossible to stain living cells with any other dye which will act as an indicator for acid.

Plant cells containing blue or purple anthocyan pigments will turn red in acids, and Pfeffer[5] found that purple *Tradescantia* or *Pulmonaria* cells become red in an "äusserst verdünnte" solution of HCl, H_2SO_4, and acetic acid, and the purple color returns when the acid is washed out; nor is the cell killed, as protoplasmic rotation also returns. The same result has been obtained by Ruhland.[6] It is difficult to judge of these results because exact molecular concentrations are not given, but they seem opposed to Bethe's experiment on medusæ. Plant pigments are difficult to work with for two reasons: (1) The plant cell is usually cuticularized and is not readily wet by the acid solution; (2) anthocyan pigments are not equally sensitive to both weak and strong acids.

The experiments recorded in this paper were all made with the tissues of a holothurian, *Stichopus ananas*, the "prickly fish" of the Beche de Mer or Trepang industry. A concentrated solution of dark-red pigment is found in irregular sacs or bodies of unknown nature just under the epithelium of practically all the internal organs. It is especially abundant on the gonads, although the eggs and sperm cells are colorless. Living portions of the testis stained in Schneider's aceto-carmine show regular epithelial nuclei and just below them the pigment bodies which have no special nuclei connected with them. Whatever their nature, acid must diffuse through an epithelium of living cells to reach them. So long as the cells are living the pigment remains in them, but if killed by heat or distilled water or chloroform-saturated sea-water or acid or alkali, the pigment passes out, *i. e.*, they cytolyse and, as in so many other pigment-containing cells, the coloring matter diffuses away.

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[1] Contributions from the Torres Straits Expedition of the Carnegie Institution of Washington and the Physiological Laboratory of Princeton University.

[2] Journ. Exp. Zool. 10, p. 507, 1911. See also Carnegie Inst. Wash. Pub. No. 183.

[3] Pfluger's Archiv, 127, p. 261, 1909.

[4] Zeit. f. Physiol. Chem., 66, p. 305, 1910.

[5] Osmotische Untersuchungen, p. 140, 1877.

[6] Jahrb. f. Wiss. Bot., 46, p. 1, 1908.

The chemical nature of the pigment is unknown. It is water soluble and fairly unstable, decomposing into brownish compounds at 100° C. If dissolved in sea-water and HCl is slowly added, it changes in color from dark red to orange when the concentration of acid becomes $n/1000$ to $n/500$. The color change is very nearly but not quite as marked in a weak acid like butyric. On the addition of alkali the color becomes purple. Moseley[1] in 1877 described a similar if not identical pigment from crinoids dredged in the channel between Cape York and Albany Island, Australia, and also from a deep-sea holothurian of the South Indian Ocean. He called the pigment antedonin and I shall adopt the same name. The echinochrome of MacMunn[2] and McClendon[3] is no doubt a closely related pigment.

Table 1.—*Temperature about 28° C.*

Concentration of acid.	Hydrochloric acid.		Butyric acid.	
	Living epithelium.	Dead epithelium.	Living epithelium.	Dead. epithelium.
$n/20$	3 to 4 mins.	Instantly.	30 secs	Instantly.
$n/40$	6 to 7 mins.	do.	15 mins	Do.
$n/80$	10 mins	do.	45 mins	Do.
$n/100$	12 mins	do.	55 mins	Do.
$n/160$	20 to 25 mins.	do.	2 hours	Do.
$n/320$	45 mins	30 secs	4 hours	1 min.

In the following experiments small pieces of the branched filamentous testis were used. Acid was added to a neutral artificial sea-water of the following composition, $m/2$ (100 NaCl+2.2 KCl+2CaCl$_2$+10MgCl$_2$), until the proper concentration of acid was obtained. Oxalic acid precipitates the Ca so that this acid was added to $m/2$ NaCl.

A study was first made of the penetration times of a weak (butyric) and a strong (HCl) acid in different concentrations into living and dead tissue. The results are given in table 1. The tissue was killed by half-minute immersion in chloroform-saturated sea-water. Under these conditions the pigment begins to diffuse out of the cells, but in each case the acid penetrates before the diffusion is nearly complete.

It will be noted that the living tissue is decidedly resistant as compared with the dead, and that the resistance varies with the acid and with the concentration of acid. Note that butyric acid in $n/20$ concentration enters more rapidly than hydrochloric, but in *n*/40 concentration the reverse is the case.

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[1] Quart. Journ. Micros. Soc., 17, p. 5, 1877.

[2] Quart. Journ. Micros. Soc., 25, p. 469, 1885; 30, p. 51, 1889.

[3] Journ. Biol. Chem. 11, p. 436, 1912.

Why does one acid enter more readily than another? To study this question we must determine the penetration rates of a large series of acids and compare them with such physical properties as degree of dissociation, power to lower the surface tension of water, solubility in lipoids, adsorbability by solids, etc. A comparison of this kind follows in table 2. All the acids enter in less than a minute if the tissue has previously been killed.

Rate of penetration into the testis of the "prickly fish" was determined from n/100 concentration of acid.

Percentage dissociation is calculated from Ostwald's[1] conductivity figures, and surface-tension values are taken from Traube's[2] results.

By lipoid solubility is meant solubility in substances of fatty nature or fat solvents—olive oil, lecithin, benzol, etc. As a measure of lipoid solubility I have determined the partition coefficient of acids between xylol/water from *n*/10 and *n*/100 concentration of acid. 25 c.c. of approximately *n*/100 acid were shaken with 25 c.c. xylol. Equilibrium is rapidly attained. The normal concentration of the acid was exactly determined before shaking and after shaking by titration. The difference is the normal concentration of acid in the xylol.

$$\frac{\text{Conc. in xylol layer}}{\text{Conc. in water layer}} = \text{partition coefficient.}$$

The determinations were only approximate, as no thermostat was used. The temperature was about 20°C. As indicated in the table, most of the acids will not pass to xylol from weak concentration in water. The values for the partition coefficients between olive oil and water were very kindly given me by Dr. Hardolph Wasteneys, of the Rockefeller Institute. The olive oil contained oleic acid equal to 2.3 c.c. *n*/100 alkali per 100 c.c. and was shaken for 15 hours with the acid solutions. The figures for adsorbability are from Appleyard and Walker's[3] experiments on silk. They represent the percentage of acid adsorbed from 100 c.c. *n*/64 acid by 3 grams of silk after 42 hours at 60°. The limit of error is one. Freundlich[4] gives a similar series for adsorption by animal charcoal.

Since the testis epithelium of the "prickly fish" is a passive tissue, the toxicity of the acids could not readily be determined on it. The cilia of the palps of the giant clam, *Tridacna gigas*, very common along the Great Barrier Reef, were therefore used for this purpose. To 50 c.c. artificial sea-water was added respectively 0.1, 0.2, 0.3, 0.4,

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[1] Organic acids. Abh. d. Sachs. Ges. d. Wissensch., 15, p. 97, 1887; inorganic acids in Journ Prac. Chem., 32, p. 300, 1885.

[2] Berichte d. d. Chem. Ges., 17, p. 2294, 1884; Verh. d. d. physikal. Ges., 10, p. 880, 1908; Liebig's Annalen, 265, p. 27.

[3] Journ. Chem. Soc., 69, p. 1334, 1896.

[4] Zeit. Physik. Chem., 57, p. 385, 1907.

TABLE 2.

Penetration rate into tissues of "prickly fish" from $n/100$ concentration.		Toxicity to cilia of giant clam. Conc. which kills in 20 hours.		Percentage dissociation of acid at $n/128$ conc.		Partition coefficient xylol/water from $n/100$ conc. at 18–22°.		Partition coefficient olive oil/water from $n/100$ conc. at 19–22°.		Surface tension of n and $n/4$ acid where water = 7.3 mg. mm.			Percentage absorption by $n/4$ conc.	
Minutes.										n	$n/4$			
½	Benzoic.	$n/2500$	Salic.	96–99	Nit.*	3.5	Caproic.	85	Caprylic.	?	?	Bens.	28	Salic.
	Salicylic.	$n/1666$	Bens.		Hydrochl.*	2.5	Bens.	34	Heptylic.	?	?	Salic.	17	Bens.
2–4	Valeric (iso).		Monochl.		Trichl.	1.3	Salic.	7.25	Caproic.		3.56	Val.	15	Hydrochl.
	Monochloracetic.		Dichl.	88	Sulph.*	0.6	Val.	6.85	Bens.	3.30	4.89	But.*	12	Sulph.
	Dichloracetic.	$n/1111$	Form.		Dichl.	0.34	σ-Amino-benzoic.	1.78	Norm. Val.	4.82		Tric.	11	Oxal.
	Trichloracetic.	$n/1000$	Trichl.	?	Oxal.*	0.1	Buty.*	0.44	But.*	4.82	6.13	Prop.*	8	Malon.
	Formic.		Sulph.*	?	Phos.*	0.02	Prop.	0.14	Prop.*	5.20		Dic.	5	Val.*
9–11	Nitric.		Tart.*	67	Maleic.*	0.015	Monochl.[1]	0.07	α Oxy-butyric.	6.00		Monoc.		Tart.
	Hydrochloric.	$n/909$	Val.*	58	Malon.*		Dichl.[1]	0.05	Acet.*	6.04	6.81	Acet.*		Citr.
	Sulphuric.	$n/833$	Nit.	35	Monochl.		Trichl.[1]	0.04	β Oxy-butyric.		7.07	Malon.*	2	Acet.
	d-Lactix.		Hydrochl.	30	Fum.	0.005	Maleic.*[1]	0.03	Succ.		7.11	Maleic.*		
	l-Lactic.		*d*-Lac.		Tart.	nil.	For.*	0.02	Form.	6.83	7.14	Form.		
12–15	Fumaric.		*l*-Lac.		Salic.*	nil.	Nit.*	0.01	Lac.		7.17	Malic.*		
	Oxalic.		Fum.		Citr.	nil.	Hydrochl.*		Cit.		7.24	Glycol.		
	Glycolic.		Glycol.	20	Malic.	nil.	Sulph.*	0.003	Tart.	7.19	7.27	Nitr.		
20	Maleic.		Maleic.	13	Form.*	nil.	*d*-Lac.*	nil.	Hydrochl.	7.25	7.28	Hydrochl.		
30	Malonic.		Malon.		Glycol.	nil.	*l*-Lac.*	nil.	Nitr.	7.27	7.30	Sulph.		
	Tartaric.		Malic.		*d*-Lac.*	nil.	Fum.	nil.	Sulph.		7.27	Oxal.		
	Phosphoric.		Cit.		*l*-Lac.*	nil.	Oxal.	nil.	Oxal.	7.27	7.29	Tart.		
40	Malic.	$n/769$	Acet.	9	Succ.	nil.	Glyc.	nil.	Malon.		7.27	Cit.		
	Citric.		Prop.	8	Bens.*	nil.	Malon.							
45–60	Acetic.		Buty.	4	Val.*	nil.	Tart.							
	Propionic.	$n/400$	Phosph.*		Acet.	nil.	Mal.							
	Butyric.				Prop.	nil.	Cit.							
					Buty.*	nil.	Acet.							
					Caproic.									
				3	σ-Amino-benzoic.									

[1] Insoluble in xylol from $n/100$ conc. in water, but slightly soluble from $n/10$ conc. as indicated by partition coefficent. The remaining acids marked nil. are insoluble even from $n/10$ conc. in water. The stronger the acid solution the more acid will pass to the xylol layer.

0.5, 0.6, 0.7, 0.8, 1.0, and 1.2 c.c. $n/10$ acid, and the concentration noted in which movement of the cilia ceased in 20 hours. To make sure that the cilia had been really killed and not simply stopped by the acid, as observed by Barratt[1] on *Paramœcium*, it was found necessary to stimulate them mechanically.

In table 2 the acids with nearly the same effect or property are arranged in groups and in an order to correspond as nearly as possible with the penetration series. An asterisk marks the acids which are markedly out of place in the series. The following acids were studied:

Benzoic,	C_6H_5 COOH = Benz.
o-Salicylic,	C_6H_4OH COOH = Salic.
(*o*-Amino benzoic,	$C_6H_4NH_2$ COOH).
Formic,	HCOOH = For.
Acetic,	CH_3 COOH = Acet.
Propionic,	CH_3 CH_2 COOH = Prop.
n-Butyric,	CH_3 CH_2 Ch_2 COOH = Buty.
iso-valeric,	$(CH_3)_2$ CH CH_2 COOH = Val.
(Caproic,	CH_3 CH_2 CH_2 CH_2 CH_2 COOH).
Monochloracetic,	CH_2Cl COOH = Monoc.
Dichloracetic,	$CHCl_2$ COOH = Dic.
Trichloracetic,	CCl_3 COOH = Tric.
Hydrochloric,	HCl = Hydroc. or Cl.
Nitric,	HNO_3 = Nitr. or NO_3.
Sulphuric,	H_2SO_4 = Sulph. or SO_4.
Phosphoric,	H_3PO_4 = Phos. or PO_4.
Oxalic,	$(COOH)_2$ = Oxal.
Malonic,	$CH_2(COOH)_2$ = Malon.
(Succinic,	C_2H_4 $(COOH)_2$).
Glycolic,	CH_2OH COOH = Glycol.
d-and *l*-Lactic,	CH_3CH OH COOH = Lac.
l-Malic,	CH_2CHOH $(COOH)_2$ = Mal.
d-Tartaric,	CHOH CHOH $(COOH)_2$ = Tart.
Citric,	CH_2 CHOH CH_2 $(COOH)_3$ = Cit.
Maleic,	C_2H_2 $(COOH)_2$ = Maleic.
Fumaric,	C_2H_2 $(COOH)_2$ = Fum.

The toxicity and effect of acids on many biological processes has been worked out, and for the sake of brevity the results have been condensed and recorded in table 3 for ready comparison with the results in table 2.

It will be noted, from table 3, that there is no agreement between the series of acids arranged in order of efficiency in affecting various tissues. Take, for example, toxicity. We might expect different organisms to vary in resistance to the same acid but the series of acids should be the same. That is, however, not the case, as a comparison of the toxicity for *Paramœcium*, for *Lupinus* seedlings, and for the cilia of the giant clam (table 2) will show. We can, therefore, state relations in only a very general way. There is a general relation between the toxicity for *Lupinus* and the giant clam, but it is not exact.

Similarly, exceptions are noted when we compare the physiological effect of the acids with their physical properties. One of the closest parallels is between the efficiency of an acid in causing membrane formation in the egg of the sea-urchin and its effect in lowering the surface tension of water. The relation was pointed out by Traube and supports his theory that the more a substance lowers the surface tension of water, the more readily it will pass into cells. Loeb had previously pointed out that the more lipoid soluble acids were most efficient in membrane formation, and suggested lipoid solubility as the determining cause of efficiency. Both of these views assume, of course, that the acids to produce their effect must enter the cells. The ability of acids to change negatively heliotropic to positively heliotropic copepods seems to depend likewise on either their surface tension or their lipoid solubility. On the other hand there are certain effects of acids which seem to depend on the strength of the acid, for instance the hæmolysis of blood corpuscles, if we can judge from the few results of Fühner and Neubauer; also the absorption of water by muscle. In these processes capillary activity and lipoid solubility play a subordinate rôle.

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[1] Zeit. f. Alleg. Physiol., 4, p. 441, 1904.

TABLE 3.

Toxicity to Paramœcium.[1]	Hæmolysis of red blood corpuscles.[2]	Toxicity for seedlings of Lupinus albus.[3]	Minimal conc. to change neg. to pos. heliotropism in copepods.[4]	Absorption of water by muscle. Per cent increase in weight in 1 hour from *n*/110 conc.[5]	Efficiency in artificial parthenogenesis of sea-urchin if butyric acid = 1.[6]
0.0001 *n* Form. Oxal. Tart. Lact. Citr. PO_4. 0.0002 *n* Cl NO_3 SO_4 Acet.	0.0005 n Cl. 0.0014 *n* Form. 0.0037 *n* Acet. 0.0065 *n* Prop. Caproic. 0.0081 *n* Val. Buty.	*n*/6400 Tric. *n*/4800 Salic. *n*/3200 Benz. Monoc. Dic. Form. SO_4. Tart. NO_3. Oxol Succ. Fum. Glycol. PO_4. Lac. *n*/1600 Maleic. Malon. Malic. Cit. Val. Prop. But. *n*/800 Acet.	*n*/500 Caproic. *n*/250 Val. Buty. *n*/200 Prop. *n*/166 Acet. For. NO_3. Cl. SO_4.	9 NO_3. Cl. 8.6 SO_4. 7.2 Lac. 7.1 Tric. 6.9 Oxal. 6.3 Tart. 5.6 Succ. 5.1 Malic. 5 Val. 5 Form. 3.9 Acet.	3 Benz. 1 Buty. <Caprylic (?) <Nonylic (?) 0.66 Prop. >Acetic (?) > For. (?) .33 Salic. .25 β Oxy-butyric. .12 Lact. .06 Oxyisobutyric. (?) Oxal. Tart. Succ. Citr. 1/100 NO_3. Cl. nil. SO_4. Only the eggs of certain females respond.

[1] Conc. which just kills in 7–30 min.; after Barratt, Zeit. f. alleg. Physiol., 4, p. 441, 1904.
[2] Conc. which just causes hæmolysis. Fühner u. Neubauer ,Arch. f. exp. Pathol., 56, p. 333, 1907.
[3] Conc. which just prevents growth. Kahlenberg and True, Bot. Gaz., 22, p. 81, 1896.
[4] Loeb, Bioc. Zeit., 23, p. 95, 1909.
[5] Loeb, Pflüger's Archiv, 69, p. 1, 1897, and 71, p. 457, 1898.
[6] Loeb, Bioc. Zeit., 15, p. 255, 1909. and Loeb, Artificial Parthenogenesis and Fertilization, p. 143, 1913.

Turning now to a comparison of the penetration rate into the tissues of the "prickly fish" with the physical properties of the acids we find again that there is no exact agreement in any case (table 2). Degree of dissociation is certainly not the determining factor in penetration, as a glance at the table will show. No one can deny but that there is a certain correspondence between lipoid solubility and capillary activity and penetration rate, yet it is far from exact. With acids as with so many other classes of substances it is only true *in general* that those compounds most soluble in lipoid penetrate most readily. This can only mean that more than one variable is concerned in determining the rate of penetration of an acid. Before discussing the second variable involved let us consider the facts in regard to the penetration of the alkalies. Note also from table 2 that the series for adsorption by silk is somewhat similar to the series for penetration rate.

Table 4 summarizes the effect of alkalies, and indicates their division into two very distinct classes, the strong and the weak. The strong always meet a marked resistance at the cell-surface; the weak meet with absolutely none and enter the cell instantly. Ability to penetrate the cell determines the toxicity of the alkali. Hence the anomalous fact that the weak alkalies are most toxic.

TABLE 4.

Strongly dissociated inorganic hydroxides, including tetraethyl-ammonium hydroxide.		More strongly dissociated weak alkalies. methyl, dimethyl, ethyl, and propyl amines.	Less strongly dissociated weak alkalies. NH_4OH and trimethyl amine.
$N(C_2H_5)_4OH$, NaOH, KOH, $Ca(OH)_2$.	$Ba(OH)_2$, $Sr(OH)_2$.		
Penetration very slow. Least toxic. Accelerate oxidation least.[1] Least efficient in causing development.[2]	Penetration slow. Less toxic.	Penetration very rapid. Most toxic. Accelerate oxidation most.[1] Most efficient in causing development.[2]	Penetration very rapid. More toxic. Accelerate oxidation less.[1] Less efficient in causing development.[2]
Lipoid insoluble. Capillary inactive.[3]		Lipoid soluble. Capillary active.	

[1] Acceleration of rate of oxidation in unfertilised sea-urchin eggs. Loeb, Journ. Biol. Chem., 14, p. 357, 1913.

[2] Efficiency in artificial parthenogenesis of the sea-urchin egg. Loeb, Artificial Parthenogenesis and Fertilization, p. 149, 1913, and Journ. Exp. Zool., 13, p. 577, 1912.

[3] *i. e.*, do not lower the surface tension of water.

Two subclasses may be distinguished under each class. If the alkali is a weak alkali, *i. e.*, belongs to the class readily penetrating, it will be more toxic the more highly dissociated it is. If the alkali belongs to the class of strong non-penetrating alkalies its toxicity will depend on the specific nature of the cation just as in the case of a salt. $Ba(OH)_2$ and $Sr(OH)_2$ are more toxic than NaOH, KOH, $Ca(OH)_2$, and $N(C_2H_5)_4OH$.

As shown by Loeb, efficiency in causing artificial parthenogenesis of the sea-urchin egg and in accelerating the oxidations in the unfertilized sea-urchin's egg run parallel with toxicity, *i. e.*, penetrability is a determining factor and degree of dissociation a secondary one.

Finally the difference between the two classes of alkalies is so marked that it seems better to speak of a resistance rather than a permeability of the cell-surface for the strong alkalies. The normal high resistance of the cell surface must then be altered by the alkali before it can enter the cell. Consequently we find that once a strong alkali has entered a cell, the cell is irreversibly injured, is, in fact, killed. Many functional activities of a cell (for instance ciliary movement or muscle contraction) cease before the strong alkali can enter. On the other hand, the weak alkalies penetrate without affecting the surface, without killing the cell, and before functional activity is appreciably affected. The easily penetrating group of alkalies are also lipoid soluble and active in lowering the surface tension of water. Data for a quantitative comparison with lipoid solubility and capillary activity are not available at present.

On comparing the acids with the alkalies several facts of interest appear. The acids form a series much more evenly graded in properties. Consequently, two classes of acids, easily penetrating and difficultly penetrating, are not so easily recognized. The acids which correspond to NH_4OH and the amines, the lipoid-soluble acids, are benzoic and salicylic with possibly valeric. The remaining acids all meet a resistance at the living cell-surface (abolished on death of the cell) which varies specifically with the acid. Once the pigment is turned red orange by the acid, removal of the tissue to sea-water does not reverse the color change. The tissue is also killed and the pigment diffuses away. Since the testis epithelium is an inert tissue, *i. e.*, contains no cilia or other indicators of functional activity, the relation between entrance of an acid and change in functional activity could not be observed.

With acids as with alkalies ability to penetrate the cell-surface appears to determine the toxicity of the acid. I am inclined to think, but can not be certain of this, that, as in the case of the strong alkalies, the lipoid-insoluble acids must destroy the normal impermeability of the cell-surface before they enter. The most toxic of the lipoid-insoluble acids would therefore be those which destroy the surface most rapidly, and they would penetrate the cell most readily for this reason also. Destruction of the cell-surface appears to depend largely on the strength of the acid, *i. e.*, its ability to combine with proteins of the cell-surface, but in part also on some specific, as yet unrecognized, peculiarity of the acid anion.

A few remarks in regard to Traube's Haftdruck theory may not be out of place. This theory depends essentially on the Gibbs-Thompson principle that a substance tending to lower the surface tension of water will collect in the surface. If a membrane is at the surface the substance will tend to pass the membrane, and always in the direction of the solution with the greatest surface tension. Difference in surface tension, "Oberflaschendruck" or "Haftdruck," determines the direction and velocity of osmosis. The more a substance lowers or increases the surface tension of water the less or the greater is its Haftdruck, and it will pass from regions of low to regions of high Haftdruck.

Originally Traube claimed that the direction and velocity of passage of a substance through a membrane were independent of the membrane and depended entirely on the Haftdruck of the solution. Had this been the case Traube's theory would have been of real value as a simple explanation of how substances pass membranes and how they enter cells, but unfortunately we know that the nature of the membrane makes a great deal of difference in determining which substances can pass it. Dead cells allow quite different substances to pass from those which living cells do. Traube now admits that the Haftdruck of the substance in the membrane is also essential. Surface tension is a measure of the Haftdruck of a solution, but we have no method of determining the Haftdruck of the substance in the membrane, so that the simplicity of the Haftdruck theory is lost. Traube now states that with certain substances even surface tension is no certain measure of the Haftdruck of a solution, a condition which still further complicates the theory (see Pfluger's Archiv, 153, p. 304, 1913).

According to Traube the lowering of surface tension (capillary activity), lipoid solubility, and osmotic velocity all run more or less parallel, but osmotic velocity is dependent primarily on capillary activity. Traube claims that capillary activity is a better measure of narcotizing power than is lipoid solubility, but our data on this point are rather scanty. The error in determining narcotic strength is large and few accurate measurements of partition coefficients have been made.

The Haftdruck of KOH is high. It slightly increases the surface tension of water, whereas the surface tension of aqueous propylamine is low. A normal solution of KOH has a surface tension ($\gamma 15°$) of 7.46 mg. mm. while *n*-propylamine = 4.63 and water = 7.3.[1] The penetrability of these two alkalies accords very nicely with the Haftdruck theory. On the other hand NH_4OH lowers the surface tension of water very little despite the fact that it enters cells with great rapidity. Thus in a capillary tube in which water will rise to a height of 91.5 mm. *n*/4 NH_4OH rises to 91 mm. while diethylamine rises to only 68.8 and piperidin to 67.5 mm. Yet NH_4OH, piperidin, and diethylamine all penetrate cells equally readily.

My results with acids give no clue as to whether lipoid solubility or capillary activity is the determining factor in penetration, since the penetration series is not in exact agreement with either lipoid solubility or capillary activity series. Wasteneys's results on the partition coefficients between olive oil and water show that the "lipoid" studied does not make very much difference. In any case butyric, propionic, and acetic acids are most out of place in the penetration series. I had fully expected them to penetrate the cells rather readily and was not a little surprised to note their position. I at first thought that they were so weak (only about 4 per cent dissociated) that the indicator (antedonin) would not detect them. This assumption can not be true, however, for valeric acid is also only 4 per cent dissociated, yet the indicator can detect it readily enough. The only other possibility is that the indicator is contained in some lipoid combination, similar in properties to xylol, within the cells of the "prickly fish." In that case a weakly dissociated acid if quite lipoid-soluble would change the color of an indicator in the lipoid, while a weak, less lipoid-soluble acid would not. This fact can be demonstrated very nicely by the use of droplets of benzol or chloroform containing Nile blue in solution. Both these fat solvents take up the dye in the red condition, while the color of the dye in acid solution is blue. If red benzol droplets of Nile blue, made by shaking the benzol solution with egg albumen,[1] are placed in *n*/10 solutions of acetic, propionic, butyric, and valeric acids, it is only in *n*/10 valeric acid that the droplets become blue. Despite the fact that valeric acid is a very weak acid, enough will enter the benzol to unite with the free red Nile blue base and form a salt blue in color. The same is true of the still weaker acid, ortho-amino-benzoic. Not enough acetic, propionic, or butyric acid can enter to do this. On the other hand a strong acid, such as trichloracetic or dichloracetic, even though very slightly lipoid-soluble, is able to cause the color change in *n*/10 concentration. Monochloracetic is not quite strong enough to do this.

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[1] Surface tension figures from Traube. J. Ber. d. d. Physik ges., 10, p. 889, 1908.

TABLE 5.

Acid.	Acetic.	Propionic.	Butyric.	Valeric.	Caproic.	Formic.	Monochloracetic.	Dichloracetic.	Trichloracetic.
Conc. for color change.	*n*/20	*n*/40	*n*/80	*n*/160	*n*/320	*n*/320	*n*/2560	*n*/5120	*n*/10240
Dissociation constant, K.	0.0078	0.0073	0.0074	0.0076	0 0014	0.0214	0.155	5.14	121.0
Partition coefficient Xylol×water from M/10 conc.	nil.	.07	.52	1.9	3.5*	nil.	.01	.01	.01

*From M/100 conc.

That both lipoid solubility and degree of dissociation are also factors in determining the color change of chloroform drops containing Nile blue is shown (table 5) when we compare the concentration of acids required to turn the drops red blue in color.[2]

The result is similar to that with benzol, except that less acid is required to change the color, due possibly to the fact that chloroform will dissolve some water in which the acids may dissociate. A strong acid (chloracetic acid and formic acid) will affect the indicator in chloroform even if very slightly lipoid-soluble, or a lipoid-soluble acid (caproic) will affect the indicator even though very weak. Carbon disulphide and carbon tetrachloride globules act similarly to chloroform globules.

However, the purple pigment of *Stichopus ananas* is certainly not in fat or oil bodies of any kind or in fat solvents. The indicator is water-soluble and no trace of the bodies holding it remains after the pigment diffuses away. We have no evidence of fat-combinations with proteins or other substances which would behave like fat solvents in the absorption of acids. There are without doubt fat or oil combinations with proteins in cells in which the physical characteristics of the fat are marked. The elaioplasts of the leaves of the vanilla orchid are the best examples. We have no visible indication that they contain fat until the cells are treated with acid when the fat appears as definite globules. Living cells behave very much as if they were droplets of oil or fat solvents.[1] This is especially well seen in the alkalies and in the narcotizing concentrations of series of alcohols and esters. The alcohol distributes itself between cell and medium as between oil and water and this is true even for plant cells which contain a minimum of lipoid material. It is quite possible that cells are largely made up of fat-protein combinations whose solubility relations are much like those of pure fat or fat solvents. At present we know nothing of such substances.

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[1] Harvey, Amer. Journ. Physiol., 6, p. 340, 1913.

[2] The series of acids for penetration into chloroform agrees to a certain extent with the penetration series for cells. The parallelism is not exact.

Any theory of permeability must explain the behavior of cells toward acids and alkalies. Why does salicylic acid enter instantly and citric acid only after 40 minutes, when both are 30 per cent dissociated? Why does ammonia enter instantly and NaOH not at all, when ammonia is a many times weaker base? Why is the effect of ammonia on cells so much greater than NaOH when, in virtue of its strength, NaOH will saponify and catalyse more rapidly, and replace the weaker NH_4OH in combination?

Without a doubt the greater physiological efficiency of ammonia is due to its greatest power of penetrating the cell, so that it acts not only on the cell-surface but the cell-interior as well. I know of no types of membranes which allow NH_4OH to pass through more readily than NaOH. Collodion, parchment, and protein films will not. Many types of protein crystals and granules and starch grains, if stained in neutral red, are found to be entered equally readily or more readily by NaOH than NH_4OH. I repeat that the cell behaves toward acids and alkalies much more as if it were a drop of benzol or xylol than a sol or gel of any ordinary protein. This unexpected fact must be explained by the assumption of some fat-like body at the cell-surface, perhaps a fat protein or a lecitho-protein, but certainly not a true fat or lecithin.

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[1] Harvey, Am. Journ. Physiol., 6, p. 341, 1913.

SUMMARY.

A pigment, "antedonin," occurs in the epithelium of the viscera of the "prickly fish," a holothurian, *Stichopus ananas*, which may be used as an indicator for the penetration of acids.

Living tissues are resistant to the penetration of all acids except salicylic, benzoic, and possibly valeric. The degree of resistance varies with the acid and is not nearly so marked as in the alkalies, which are compared with the acids.

The penetration rate of HCl is roughly proportional to the concentration. Dead tissues are readily permeable for all acids.

There is no relation between the degree of dissociation of the acid and its rate of penetration or between degree of dissociation and toxicity.

There is a general relation between penetrability and lipoid solubility and capillary activity, but it is not exact and not quantitative.

The best relation is between penetrability and toxicity. The acids which penetrate most readily are most toxic, irrespective of their strength.

With acids as with alkalies lipoid solubility or capillary activity appears to be a determining factor in penetrability. No distinction can be drawn between these two possibilities, since the penetration series is not in exact agreement with either lipoid solubility or surface-tension series. Acetic, propionic, and butyric acid are most out of place and it is suggested how this might be explained if the indicator were dissolved in a fat solvent or the cell as a whole acted as a fat solvent.

If an acid is soluble enough in fatty substances, it encounters no resistance at the cell-surface; if it is lipoid-insoluble or only slightly soluble the normal cell-surface must be destroyed before it can enter. The strength of the acid and possibly also a specific action of the anion on the surface protein will then determine its rate of entrance, or, better, its rate of alteration of the cell-surface.

Cells behave toward acids and alkalies as if they were droplets of a fat or fat solvent, which suggests that they must be composed largely of fat-protein combinations in which the visible physical characteristics of fat are masked.

VII.

MEDUSÆ OF THE PHILIPPINES AND OF TORRES STRAITS.

BEING A

REPORT UPON THE SCYPHOMEDUSÆ COLLECTED BY THE UNITED STATES FISHERIES BUREAU STEAMER "ALBATROSS" IN THE PHILIPPINE ISLANDS AND MALAY ARCHIPELAGO, 1907-1910, AND UPON THE MEDUSÆ COLLECTED BY THE EXPEDITION OF THE CARNEGIE INSTITUTION OF WASHINGTON TO TORRES STRAITS, AUSTRALIA, IN 1913.

BY ALFRED GOLDSBOROUGH MAYER,
Director of the Department of Marine Biology of the Carnegie Institution of Washington.

Three plates and seven text-figures.

MEDUSÆ OF THE PHILIPPINES[*] AND OF TORRES STRAITS.

BY ALFRED GOLDSBOROUGH MAYER.

INTRODUCTION.

In 1909, Dr. Hugh M. Smith, the then Acting United States Commissioner of Fisheries (now Commissioner), gave to the author for study a part of the collection of medusæ now under consideration in this article, and the authorities of the Smithsonian Institution kindly permitted the use of a table in the building in Washington while engaged upon this work. In 1910 another part of the collection was sent to Princeton University, where the author occupied a research room in Guyot Hall. Thus the collection was studied under the most advantageous conditions and it is a pleasure to express my sense of indebtedness to the authorities of the United States Bureau of Fisheries, the Smithsonian Institution, and Princeton University for the opportunities I have enjoyed.

In September and October 1913 the writer was leader of the expedition sent by the Carnegie Institution of Washington to Torres Straits, Australia, and spent five weeks on the Murray Islands, about 70 miles south of the New Guinea coast and within 6 miles of the seaward edge of the Great Barrier Reef of Queensland.

Thirty-one scyphomedusæ were obtained by the *Albatross* in the Philippines and adjacent regions, the list of species being as follows:

CARYBEIDÆ.

Carybdea rastonii Haacke.
Carybdea alata var. grandis Agassis and Mayer.
Chiropsalmus quadrigatus Haeckel.

CORONATÆ.

Periphylla hyacinthina Steenstrup.
Linuche unguiculata forma aquila.
Atolla bairdii forma wyvillei Haeckel.
Atolla bairdii forma gigantea Maas.
Atolla bairdii forma valdiviæ Vanhöffen.

SEMÆOSTOMÆ.

Pelagia panopyra Péron and Lesueur.
Chrysaora melanaster Brandt.
Dactylometra africana Vanhöffen.
Sanderia malayensis Götte.
Discomedusa philippina Mayer.
Aurellia aurita Lamarck.
Aurellia labiata Chamisso and Eysenhardt.

RHIZOSTOMATA.

Cassiopea andromeda var. baduensis, nov. var.
Cephea octostyla (Forskål).
Cephea cephea var. cœrulea Vanhöffen.
Cotylorhiza pacifica, sp. nov.
Catostylus purpurus Mayer.
Catostylus townsendi, sp. nov.
Catostylus mosaicus L. Agassis.
Lychnorhiza bartschi Mayer.
Lychnorhiza bornensis, sp. nov.
Mastigias papua L. Agassis.
Mastigias ocellata Haeckel.
Phyllorhiza lusoni, sp. nov.
Versura maasi Mayer.
Lobonema smithii Mayer.
Thysanostoma thysanura Haeckel.
Lorifera lorifera var. pacifica Schultse.

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[*] Published by permission of Hon. Hugh M. Smith, U. S. Commissioner of Fisheries.

It is evident that the region of the Philippines* is very rich in scyphomedusæ, for off the far better-known Atlantic coast of the United States there are but 25 species of scyphomedusæ and only 4 of these are Rhizostomæ, while among the 38 species taken by the *Albatross*, and by Light, in the region of the Philippines, 22 are Rhizostomæ. Among these 38 species 15 were new to science.

The discovery of a *Cotylorhiza* allied to the form known from the Mediterranean is interesting, but the most curious Philippine genus is *Lobonema*, wherein the marginal lobes of the bell are greatly extended and superficially resemble tentacles tapering gradually throughout their length to pointed tips. They are, however, not capable of contraction and their function is problematical.

It appears that in Borneo and the Celebes, some of the Scyphomedusæ are specifically distinct from their close relatives found in the Philippines, the difference probably being due to geographical isolation. As the *Albatross* collected only conspicuous forms of scyphomedusæ, and as several species are represented by only one or a very few specimens, it seems probable that further studies in the region would be fruitful in discoveries, and in any event the forms should be studied in life, for much that is of interest is lost through the effects of preservative fluids.

By contrast with the richness of the Philippines, the poverty of the Great Barrier Reef of Queensland and the southern coast of Papua, east of Torres Straits is remarkable, for only six species of scyphomedusæ and ten of hydromedusæ were found by the expedition of the Carnegie Institution of Washington to Torres Straits, as follows:

SCYPHOMEDUSÆ.

Aurellia labiata Chamisso and Eysenhardt; Thursday Island, Torres Straits.
Cassiopea andromeda var. baduensis, nov. var.; Badu Island, Torres Straits.
Catostylus mosaicus L. Agassiz; cobalt blue, from the mouth of the Brisbane River, Queensland.
Linuche unguiculata forma aquila Haeckel; from Thursday Island, Torres Straits, November 23, 1913.
Mastigias papua L. Agassiz; Port Moresby Harbor, Papua, November 12–20, 1913.
Nausithoë punctata Kölliker; from Torres Straits and the southeast coast of Papua.

HYDROMEDUSÆ FROM THE MURRAY ISLANDS.

Æquorea macrodactyla (Brandt).
Aglaura hemistoma Péron and Lesueur.
Cytæis atlantica (Steenstrup).
Eutima australis, nov. sp.
Laodicea fijiana A. Agassiz and Mayer.
Liriope rosacea Gegenbaur.
Phialidium pacificum (Maas).
Rhopalonema velatum Gegenbaur.
Solmundella mediterranea (Müller).
Stomotoca turrida (Mayer).

During September and October 1913, we studied for 5 weeks upon Maër Island, about 70 miles south of Papua; using a naphtha launch and towing with surface nets under the best conditions, but the results are remarkable only for their poverty.

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*S. F. Light, 1914, Philippine Journal of Science, vol. 9, No. 3, describes 7 species from the Philippines other than those obtained by the *Albatross*. Mr. Light's additional species are *Dactylometra quinquecirrha*, *Cassiopea polypoides*, *Cassiopea medusa* sp. nov., *Acromitus maculosus* gen. et sp. nov., *Lobonema mayeri* nov. sp., *Lobonemoides gracilis* gen. et sp. nov., and *Rhopilema visayana* nov. sp.

Only one Scyphomedusa (*Catostylus mosaicus*) and one hydromedusa (*Eutima australis*, nov. sp.) are possibly peculiar to Australia; all the others are of wide distribution. Of the six Scyphomedusæ which we collected, two are widely distributed over the Pacific and three others are known both from the tropical Atlantic and the Pacific. Similarly, of the ten hydromedusæ, three are widely ranging Pacific species and six others are found in both the Atlantic and Pacific. It appears that along the east coast of Queensland and the southeast coast of Papua is one of the poorest regions in the tropical world for medusæ, containing almost nothing peculiar to itself; whereas the region of the Philippines and northern shores of New Guinea is one of the richest. This appears to be another illustration of the influence of a great ocean current, the rich region of the Philippines being in the sweep of the Japan Stream, whereas there is no well-defined current along the southern shore of Papua or off the Barrier Reef of Queensland. As is well known, H. B. Bigelow, in his report upon the siphonophoræ of the *Albatross*, shows how abundant these forms are in the Humboldt current off the west coast of South America and how poor the region is in the mid-Pacific to the westward of this great current. Our studies made while assistant upon Dr. Alexander Agassiz's expeditions to the tropical Pacific, as well as upon the recent expedition to Torres Straits and Papua, show that the whole great belt of the South Tropical Pacific, from the western edge of the Humboldt current to the shores of Australia, is poor in pelagic life. A number of local medusæ appear in some of the large island groups, as in Fiji, but the region as a whole is poor in forms peculiar to itself and even those of wide distribution are, generally speaking, found only occasionally over this great desert of ocean.

While in Australia we saw no swarms of Scyphomedusæ other than a great number of specimens of the cobalt-blue form of *Catostylus mosaicus* L. Agassiz, in the estuary of the Brisbane River, Queensland, in September. These medusæ appeared to be of all sizes, and as we saw them also in April and May 1896 in the same locality they may possibly breed throughout the year.

A single specimen of a variety of *Cassiopea andromeda* was found at Badu Island in Torres Straits, and *Mastigias papua* was common in the harbor of Port Moresby, Papua, in November.

Aurellia labiata was occasionally seen in Torres Straits, and this scyphomedusa is known only from the Pacific; but on July 27, 1913, a perfect adult specimen, intermediate in character between *A. aurita* and *A. labiata*, was found at Tortugas, Florida. A detailed description of this individual will be found in the text of this article. In this connection it will be recalled that Vanhöffen finds that the Pacific form of *Linuche*, called *L. aquila*, appears also as a variety of the *Linuche unguiculata* of the tropical Atlantic, and it seems possible that in *Aurellia* the common *A. aurita* of the Atlantic may occasionally give rise to *Aurellia labiata* as a mutation, and that the Pacific species arose in this manner.

We will now give a brief account of the characters of the Scyphomedusæ.

STRUCTURE, PHYSIOLOGY, HABITS, AND DEVELOPMENT OF THE SCYPHOMEDUSÆ.

The Scyphomedusæ are the large jellyfishes, commonly called the sea-blubbers, in which the body is umbrella-shaped, the mouth parts occupying the position of the handle of the umbrella. The animal swims by means of a periodic expansion and contraction of the margin of the umbrella. If we look carefully we will see that this margin is notched at regular intervals, forming a series of lappets, and that 8 or sometimes 16 of these notches are deeper than the others and contain each a minute finger-shaped or club-shaped sense-organ which may be provided with an eye, but which always contains a mass of crystals or concretions concentrated at its outer end. These little sense-organs are so small that they appear to the naked eye as mere pigmented specks placed within the niches at regular intervals around the margin; but small as they are they are of vital importance to the jellyfish, constituting its principal nerve centers, and if we cut them off, the animal commonly becomes paralyzed and is no longer able to pulsate spontaneously. Mayer believes that the crystals or concretions within the sense-clubs consist largely of calcium oxalate, and this makes it appear probable that sodium oxalate is constantly forming in the sense-club and that the calcium chloride of the sea-water, when it enters the sense-clubs, is precipitated, forming calcium oxalate, and in this manner setting free sodium chloride (common salt), which is a powerful stimulant for the nerves, thus causing the pulsating reaction.

Thus in these animals we find that a stimulus which is constantly present causes periodic contractions followed by periods of rest which are perhaps due to fatigue. In the case of the scyphomedusa *Cassiopea* this stimulus is internal, for the sea-water itself neither stimulates nor inhibits the sense-organs of the animal, the stimulating effect of the interaction of its sodium, potassium, and calcium being offset by the inhibiting effect of its magnesium upon the motor centers.

But the marginal sense-organs do more than merely produce the pulsation stimulus, for Dr. L. R. Cary finds that if they be removed and the medusa be wounded in any manner the first stages in regeneration are slow, but if even a single sense-organ be present regeneration proceeds at once and with rapidity.

In general, if the area of tissue enervated by a sense-organ be large it pulsates more rapidly than if the area be small, and although the ratio is not strictly proportional to the area of tissue, yet we may still say that if a sense-organ be cut off with only a small piece of tissue around it the rate of pulsation will be much reduced. But young, small jellyfishes pulsate more rapidly than large old ones, yet if we graft two jellyfishes together the small active one will force the large one to pulsate at its own rate, which will be even more rapid than the normal rate of the small one, due to the large area of tissue the sense-organs now control.

Eimer and Romanes found that if the marginal sense-organs be removed the jellyfish is paralyzed and responds only by single contractions to external stimuli. Later, in 1906, Mayer found that if the sense-organs be removed and we cut a ring-shaped, or *complete circuit* shaped, strip of tissue from the concave part of the bell, we may then start a contraction wave proceeding in *one direction* through the circuit through which it travels continuously, being indeed entrapped by the circuit of tissue from which it can not escape. This movement is almost machine-like in its regularity, and very different from the slow and somewhat irregular pulsations the sense-organs engender.

It is interesting to see that the pulsation stimulus in jellyfishes is conducted by the nerves, whereas in the vertebrate heart it is conducted by the muscles. There is, however, as Parker showed, a fundamental likeness between nervous and muscular activity, for in most essential features, such as the compensating pause following an extra pulsation and the refractory stage during systole, latent period, reaction to temperature, etc., the jellyfishes behave as does the vertebrate heart. In Europe Romanes, Bethe, and von Uexkull, and in America Loeb and Mayer have been most active in these studies.

Recently Mayer finds that nerve conduction in *Cassiopea* is a chemical reaction in which the cations of sodium, calcium, and potassium take the active part, while magnesium is passive. The sodium calcium and potassium appear to be attracted by adsorption to the surfaces of some negatively charged colloidal elements of the nerve, and the velocity of nerve conduction is proportional to the degree of concentration of these adsorbed cations.

Thus if V be the velocity of nerve conduction, and C be the concentration of the sodium calcium and potassium cations in the surrounding sea-water, then for all dilutions down to sea-water mixed with an equal volume of distilled water $V=2.0\ C^{0.86}$ where the velocity of nerve conduction and the concentration of the cations in natural sea-water are both 100.

It is remarkable, as Goldfarb showed, that a jellyfish such as *Cassiopea* regenerates more rapidly in 90 per cent sea water (90 parts of sea-water mixed with 10 parts of distilled water) than it does in normal sea-water.

In all scyphomedusæ excepting the Rhizostomæ tentacles are found at the bell-margin, and usually grow out from between the notches of the rim. These tentacles are hollow, the stomach cavity being continued into them as it is also into the sense-clubs; indeed, there is every reason to believe that the sense-organs are only highly modified tentacles.

Powerfully developed circular, or a combination of circular and radial, muscles are found in the under, concave part of the umbrella, and here also there is a network of nerve-fibers connecting the muscles with the sense-clubs. Curiously, there are no muscles, and probably no nerves, over the outer convex part of the umbrella.

Those who have handled jellyfishes know that they are capable of inflicting a sharp sting, the tentacles being especially active in this respect. Closely clustered over the surface of the tentacles, and other parts of the jellyfish, there are minute cells, each containing a hollow tube coiled rope-like within the cell. Upon excitation these little tubes are turned inside out and shot forward, and their outer ends, which are barbed, penetrate the skin, causing a sharp sting due in part, it appears, to formic acid. Thus it is that these large jellyfishes are among the most persistent enemies of the fishes, for many an incautious victim is ensnared among their stinging tentacles only to be paralyzed and finally drawn upward into the mouth of the jellyfish. It is, however, a poor rule which does not work in both directions, and certain kinds of small fishes often accompany the jellyfishes, swimming in and out among the dangerous tentacles, even biting off small pieces of the jellyfish itself and occasionally themselves falling a prey to the stings, but in general enjoying a peculiar protection from the attacks of larger fishes who dare not venture too near the jellyfish.

The mouth, or mouths, of the jellyfish may be surrounded by veil-like lips or, if the mouths are numerous, as in the so-called Rhizostomæ (root-mouthed) jellyfishes, by complex frills lined by minute tentacles which at intervals bend to and fro and sweep, as it were, for food, for the jellyfishes are all carnivorous. In the higher animals the intestine is a tube which lies suspended within the body cavity, but as long ago as 1849 Huxley showed that the jellyfishes have no body-cavity, and consist simply of a stomach and an outside with a mere structureless lamella, or a solid mass of jelly, between the stomach-wall and the outer skin layer of the animal.

This gelatinous substance may serve as a store of food for the animal in case of starvation, and *Cassiopea* can live at least 42 days without food, the weight of the jellyfish declining to less than one-hundredth its original magnitude. The loss of weight on each day is, however, proportional to the weight of the animal at the beginning of that day and thus the lighter it becomes the less the weight lost.

Thus, if W be the original weight of the jellyfish, and y its weight after x days of starving, then $y = W\ (1-a)^x$; where a is a constant, less than unity.

Indeed the ultimate size that an individual jellyfish attains before becoming mature is a measure of its success in obtaining food, and it is interesting to see that the largest jellyfishes are those of the cold seas where the floating animal life is more abundant than in the tropics. In common with the corals, sea-anemones, alcyonaria, siphonophores, and hydromedusæ the scyphomedusæ are, so far as is known, exclusively carnivorous and do not feed upon plant life.

The prey is seized by the mouth, and after being held and partially digested in the stomach the remnant is ejected through the mouth.

The central stomach is a space in the middle of the umbrella, but this always gives rise to an outwardly radiating system of pouches or tubes which may form a complex network of vessels under the muscular layer of the concave side of the umbrella. As this system of pouches is connected with the stomach and nutrient fluids derived from the food circulate through it, it is often called the gastrovascular system, for it is both a sort of "chymiferous system" and a digestive space.

In all of the larger jellyfishes, or scyphomedusæ, we find within the stomach 4 clusters of tentacle-shaped organs of unknown function, placed at the broad sides of the cruciform mouth. The smaller jellyfishes, or hydromedusæ, lack these stomach-tentacles or gastric cirri as they are often called, and in still another structural detail do they differ from the scyphomedusæ, for the hydromedusæ have a diaphragm-like membrane which grows inward from the bell-margin and partially closes the opening of the umbrella, but the larger jellyfishes (scyphomedusæ) do not have a diaphragm of this sort, although it is true that the Cubomedusæ, or sea-wasps, appear to have such a diaphragm, but it is not strictly comparable with that of the hydromedusæ.

The sexual organs of the larger jellyfishes (scyphomedusæ) are found in the stomach peripheral to, and closely associated with, the four clusters of gastric cirri. The sexes are usually separate, the animals being either male or female, although in rare instances, as in *Chrysaora*, they are hermaphroditic, or male when young and female when old. When mature at the breeding season the males and females usually come to the surface in great numbers and may congregate in vast swarms many square miles in area. The larvæ or eggs may then be cast out into the water by the breaking down of the stomach-wall or the larvæ may undergo a part of their development within the stomach, or mouth-parts, of the mother, finally to be cast out through the mouth.

In any event the larvæ soon develop into minute pear-shaped creatures about as large as a pin's head, their bodies being covered with vibrating cilia which enable them to spin through the water. For a few days or even weeks they may remain thus swimming near the surface and be drifted far by tide and ocean current. Soon, however, the little pear-shaped planula, as it is called, settles down head first upon the bottom and fastens itself to some fixed object. Then for the first time the mouth develops at that which was the posterior end of the planula and tentacles grow out so that the mouth is soon surrounded by 16 or more of these organs which serve to capture the minute crustacea and other organisms upon which the little polyp feeds. Thus it remains sedentary for a long period, growing all the time and superficially resembling a small sea-anemone. Finally a series of constrictions develop at regular intervals, and the creature appears as if it were composed of a series of disks set one upon the other. The margin of each disk soon develops 8 cleft lobes, and 8 sense-clubs appear in the clefts. Then the uppermost disk, containing the mouth and the crown of tentacles, is cast off and perishes, while the others are set free in succession and swim away as minute jellyfishes, soon to develop tentacles and finally to become mature and repeat this peculiar process of development. After the last disk has been cast off, only the stump of the strobila, as it is called, remains, but this may regenerate a new ring of tentacles and continue to grow, possibly to develop more jellyfishes at the succeeding season.

There are many interesting variations of this typical process of development. Often the strobila, instead of giving off a series of disks, develops only a single constriction and every alternate tentacle changes into a sense-club, while the other tentacles may be wholly absorbed, so that they disappear. In this case only a single ephyra or larval jellyfish is set free. This form of development is especially characteristic of the Rhizostomæ or multi-mouthed jellyfishes, such as *Cassiopea*. In the free-floating *Pelagia*, however, the planula larva never becomes attached, but remains swimming through the water until it develops directly into a jellyfish. Thus it is that these jellyfishes are quite independent of the land and are widely distributed over the tropical and warm oceans.

Several other sorts of jellyfishes are widely distributed over the world, one of these being the large semi-transparent *Aurellia aurita* of our coast, which appears so commonly during the summer and may be recognized by its 4 horseshoe-shaped, milky or pink-colored genital organs. This form occurs from pole to pole.

Such adaptability to wide range of temperature is very rare among jellyfishes, and is known only in *Aurellia aurita* and *Nausithoë punctata* among the scyphomedusæ, and *Solmundella* among hydromedusæ, these forms occurring in seas of all temperatures.

Nevertheless, even tropical medusæ are much more injuriously affected by a slight rise in temperature than are the jellyfishes of the temperate regions, and we may say that most tropical forms live within 12° C. of their heat-death-temperature, and even tropical forms can withstand cooling better than they can resist heat. To use an engineering expression we might say that the medusæ of temperate regions have a larger "factor of safety" in respect to temperature. Harvey showed that, upon heating, the rate of conduction of the nervous stimulus which causes pulsation increases in an arithmetical ratio, so that its "curve" is a straight line. At from 34° to 39°, however, the curve makes a sudden bend downward and the rate declines sharply. This decline may be due to the effects of asphyxiation, for Winterstein showed that the rate of oxygen consumption in jellyfishes is 3½ times as rapid at 30° to 35° as it is at about 12° C. Thus the oxygen of the sea-water becomes insufficient to support the augmented vital activities of the animal.

The large, rich rosin-brown colored cyaneas of our New England coast are not found in the tropics, but closely allied species reappear in the south temperate zone, so that somehow they have managed, perhaps in the glacial epoch, to cross the warm zone of the tropics. Yet another set of forms, which are widely distributed over temperate and warm seas, are creatures closely allied to the *Dactylometra* of the southern shore of New England and southward, a jellyfish which may be recognized by the reddish brown or purple radial streaks upon the umbrella and its long, graceful, folded, curtain-like lips often beautifully tinged with pink.

We may distinguish five main divisions or orders of the larger jellyfishes or scyphomedusæ.

I. The *Carybdeidæ* or *Cubomedusæ*, with bell almost rectangular and with flexible tentacles mounted upon the ends of gelatinous wing-shaped expansions. They have 4 knob-shaped sense-clubs, which are very large and set within niches on the sides of the bell, with the eyes all directed inward, apparently to command a view of the mouth. These medusæ have a marginal diaphragm which partially closes the opening to the umbrella cavity. The Carybdeidæ are confined to tropical and warm seas and usually remain upon or near the bottom until they become mature, when they often swim to the surface to cast out their eggs and sperm. They are usually dull milky-yellow or livid in color, and their tentacles sting so sharply that they are commonly called sea-wasps. None are known north of Cape Cod, but they are well represented in the tropics throughout the world.

II. The *Stauromedusæ* are attached forms which do not pulsate. The body is pear-shaped or pyramidal and the jellyfish fastens itself to sea-weed or rocks by means of a stalk at the aboral end of the body. There are usually 8 clusters of knobbed tentacles which are developed at the pointed ends of 8 marginal lobes, and 8 large "anchors" or sucker-like clubs upon the margin may alternate with the tentacles. These forms are confined to cold seas and are known from the Arctic and Antarctic Oceans, although they have never been found in the tropics.

III. The *Coronatæ* are usually deep-sea forms distinguished by their peculiar dark purple or reddish-brown color, which is so characteristic of the invertebrate animals of the deep sea, due possibly to the fact that the red rays from the sun are rapidly absorbed as they penetrate into the depths of the ocean, so that at depths greater than 1,000 fathoms there is practically no red light, and here red-colored animals must appear black and be well concealed in the general darkness of their abysmal realm. The Coronatæ are characterized by having a deep ring-like furrow cutting into the thick wall of the sides of the umbrella; and peripheral to this are gelatinous thickenings in the radii of the tentacles and sense-organs. The gelatinous wall of the bell is much reduced in thickness at the ring-furrow, the thin part acting as a hinge to permit the creature to close its bell during contraction. These forms are common in the deep waters of the Philippines, as indeed they are upon the bottom of all seas 500 fathoms or more in depth. Most of the species, such as *Atolla* and *Periphylla*, do not normally come to the surface, but a closely allied form, the little *Nausithoë*, is one of the most universally distributed surface forms of all warm seas, while the mature *Linuche* occur in vast numbers, all rapidly pulsating and resembling little brown thimbles, the swarm often covering square miles of ocean in tropical regions.

IV. The *Semæostomata* are the common large jellyfishes of our coasts, such as *Aurellia*, *Cyanea*, and *Dactylometra*. They have tentacles and a single cruciform mouth provided with veil-like lips, and there is no ring-furrow cutting into the surface of the umbrella, such as is seen in the Coronatæ. They are common in bays and brackish estuaries and are the largest and most conspicuous of all jellyfishes in temperate regions.

V. The *Rhizostomæ* are the large jellyfishes of the East Indian and tropical seas, where they are commonly as conspicuous as are the Semæostomeæ in our cold northern waters. They have numerous mouths and no tentacles, and their gelatinous substance is often as rigid as newly formed cartilage. Often they occur in swarms in the harbors, swimming strongly against the tide, and after a storm great numbers are found stranded upon the shore. The rigid gelatinous substance of these jellyfishes is very characteristic and was seen in fossil forms found in the Jurassic lithographic slates of Steinheim in Bavaria, showing that in the age of the Reptiles these most highly differentiated jellyfishes existed. Indeed, so old are the jellyfishes that their relationship to the echinoderms, sponges, and ctenophores remains unknown—all intergrading forms, if such ever existed, having died out long ago, as is often the case in very ancient orders.

In an early stage of development the higher animals commonly pass through a condition in which they have only an outer cell-layer and a cavity lined by cells destined to form the intestine. Theoretically speaking, they are simply little 2-layered sacks, the outer layer being the external skin with its nervous and sensory organs, and the inner layer being the stomach; and thus the name gastrula is applied to this stage. Jellyfishes are essentially in the gastrula stage even when adult. Yet so extraordinary are the foldings and outgrowths that have arisen in their two body-layers during the vast time they have existed upon the earth that, ultimately simple as they are, no class of the animal kingdom exhibits a more surprising variety of forms than do the jellyfishes and their close allies the Siphonophoræ.

It is interesting to observe that the large jellyfishes, scyphomedusæ, which have gastric cirri and no marginal diaphragm or velum, are probably only very remotely related to the small jellyfishes, the hydromedusæ, which have a velum and lack gastric cirri. Indeed we have good reason to believe that the jellyfish-shape and peculiar locomotion through pulsation have been derived independently in the two groups. The scyphomedusæ are probably allied to the actinians or sea-anemones, while the hydromedusæ have probably been derived from hydroids. In fact a jellyfish-like shape and pulsating body have been acquired independently in widely different kinds of animals, such as *Pelagothuria*, a holothurian which bears a wonderfully close resemblance to a jellyfish and swims actively through the water in the tropical Pacific; and in *Craspedotella*, a minute unicellular marine animal, which would certainly have been mistaken for a jellyfish had it not been of microscopic size.

Indeed there is reason to lead us to believe that the bell of the Narcomedusæ is a mere outgrowth from the sides of the pyriform larva, and has thus been acquired in a manner quite different from that of the other hydromedusæ. Thus the umbrella-like bodies of jellyfishes have probably been acquired in at least three different ways within the group itself.

PART I.

SCYPHOMEDUSÆ OF THE PHILIPPINE ISLANDS.

DESCRIPTION OF SPECIES.

Through the kindness of Dr. Hugh M. Smith, then Deputy Commissioner, now Commissioner, of Fisheries of the United States, the author was permitted to describe and figure some of the *Albatross*-Philippine scyphomedusæ in volume III of "Medusæ of the World," published by the Carnegie Institution of Washington in 1910. These are referred to, but are not here redescribed, unless some new facts have come to light since the date of the original description.

Genus CARYBDEA Péron and Lesueur, 1809.

Carybdea, PÉRON ET LESUEUR, 1809, Ann. Mus. Hist. Nat., Paris, tome 14, p. 332.—MAYER, 1910, Medusæ of the World, vol. 3, p. 506.

GENERIC CHARACTERS.

Carybdeidæ with 4 simple, interradial tentacles and pedalia. Velarium supported by 4 bracket-like frenulæ. Velar canals present. Stomach small and 4-sided.

Carybdea rastonii Haacke.

Carybdea rastonii, HAACKE, 1887, Jena. Zeitsch. für Naturwissen. Bd. 20, p. 591, Taf. 35, Figs. 1–15.—MAYER, 1910, Medusæ of the World, vol. 3, p. 508.

There are two specimens of this medusa in the *Albatross* collection from the Philippines. They are apparently mature and their dimensions in millimeters are as follows:

	Locality and date.	
	Subig Bay, Luzon, surface, Jan. 6, 1908.	Taal Anchorage, Balayan Bay, Luzon, surface, Feb. 20, 1909.
Height of bell	34	33
Width of bell	20	23.5
Length of pedalia	11	9.5
Width of pedalia at base	....	4
Width of pedalia at widest part	6.5	5.5
Height of sensory niche above velar margin	6	6
Length of flexible shafts of tentacles	30	66

This is the commonest Cubomedusa of the tropical Pacific, being widely distributed from South Australia to the Hawaiian Islands. It can be recognized by its prismatic, 4-sided bell, the pedalia being about one-fourth to one-third as long as the bell-height, flat and spatula-shaped and about three-fifths as wide as long. The sense-clubs have each 2 large median eyes and 4 small lateral ocelli. There are 4 short, branched, non-anastomosing velar canals in each quadrant of the velarium, 16 in all. Four very small branched tufts of gastric cirri. This medusa is very closely allied to *Carybdea marsupialis* of the Mediterranean, but is distinguished by having only 16 instead of 24 to 30 canals, and by its somewhat more slender pedalia. In both forms the bell is dull milky yellow and the flexible parts of the tentacles are pink. In common with other Cubomedusæ it comes to the surface when mature, and is then abundant in harbors. The young usually remain in deep water at or near the bottom.

Carybdea alata var. grandis Agassiz and Mayer.

Carybdea grandis, Agassiz and Mayer, 1902, Mem. Museum Comp. Zool. at Harvard College, vol. 26, p. 153, plate 6, figs. 26–31.

Carybdea alata var. *grandis*, Mayer, 1910, Medusæ of the World, vol. 3, p. 511, fig. 329.

The bell of this medusa becomes 230 mm. high, but the largest specimen of this cruise was obtained by the *Albatross* in Borneo and is only 166 mm. high. This tropical Pacific form may be distinguished by its short, wide-flaring pedalia and by having only 1 or 2 median eyes upon each sense-club and no lateral eyes. When young, however, there are 2 large median and 2 small lateral eyes, but the latter appear to fuse later with the median eyes. There are 24 velar canals, which are short, branched, and non-anastomosing. *C. moseri* is probably only a young stage of this medusa. In *C. alata* there are 6 eyes in each sense-club, and the pedalia are longer and narrower than in the large variety *grandis*.

The dimensions and characters of the two largest of the three specimens found by the *Albatross* are as follows:

	Locality, date, and number of specimens.	
	Station 5361, Feb. 9, 1909, Manila Bay, Luzon, 12 fathoms, 2 specimens.	D. 5594, Sept. 30, 1909, off Mount Putri, Borneo.
Height of bell	120	166
Width of bell	88	144
Length of pedalia	38 along inner side.	77 along outer side, 36 along inner side.
Width of pedalia at widest part	16.5	29
Width of pedalia at base	14	
Height of sensory niche above velar margin	16	31
Number of eyes in each sense-club	2 median, no lateral eyes.	2 median, no lateral eyes.
Gonads	Small, immature.	Small.

Genus CHIROPSALMUS L. Agassiz, 1862.

Chiropsalmus, Agassiz, L., 1862, Cont. Nat. Hist. U. S., vol. 4, p. 174.

GENERIC CHARACTERS.

Carybdeidæ with 4 interradial, branching pedalia which give rise to a number of tentacles. Four wide perradially situated stomach-pockets in the subumbrella, each of which gives rise to finger-shaped, unbranched, hernia-like pouches which project into the bell-cavity. Wide, marginal pouches and numerous canals in the velarium. 8 leaf-shaped gonads.

Chiropsalmus quadrigatus Haeckel.

Chiropsalmus quadrigatus, Haeckel, 1880, Syst. der Medusen, p. 447.—Mayer, 1910, Medusæ of the World, vol. 3, p. 516, fig. 331.—Light, 1914, Philippine Journ. Science, vol. 9, p. 197.

44 specimens of this medusa were collected by the *Albatross* from the Philippines, but not one seems to be mature.

Light (1914) found this medusa at Culion Bay, Culion, and at Palawan and thus it ranges widely in the Philippines. Light's specimens were larger than those found by the *Albatross*, being at least 200 mm. in diameter and usually with 7 tentacles to each pedalium. The tentacles are 1.5 meters or more in length and have lavender-colored bands of nematocysts. Light reports that the sting of this medusa is very severe and may even be fatal to man. The *Dactylometra* of the Philippines is also a dangerous form, but *Lobonema*, which some of the members of the *Albatross* expedition believed to be virulent, is not capable of inflicting a very severe sting (see Light, 1914, Philippine Journal of Science, vol. 9, pp. 291–295).

The following is a record of specimens of *Chiropsalmus quadrigatus* obtained by the *Albatross* in the Philippine Islands:

Locality.	Date.	Height of bell in mm.	Width of bell in mm.	Number of tentacles upon each pedalium.	Remarks.
Subig Bay, Luzon, caught in a seine.	1908 Jan. 7	18	20	4, 4, 4, 4	No gastric saccules and no gonads.
Do	Jan. 7	70	80	9, 5, 8, 8	With well-developed but immature gonads; large cock's-comb-shaped gastric saccules.
Cataingan Bay, Masbate, near shore.	Apr. 18	49	55	6, 6, 7, 7	Immature. The 8 gastric saccules only beginning to appear.
Do	Apr. 18	51	51	8, 6, 7, 5	Do.
Do	Apr. 18	40	20	6, 5, 6, 6	Do.
Mausalay, Mindanao	June 4	97	100	8, 8, 8, 8	Apparently mature.
Point Janelo, Southern Luzon, one specimen.	July 13	......	......	......	Immature. Caught in a seine at a depth of 150 feet.
Tilig Bay, Southern Luzon, one specimen.	July 14	......	......	......	Immature. Caught in a seine at a depth of 130 feet.
Malcochim Harbor, Linapacan Island, 7 specimens.	Dec. 18	86	95	6, 7, 8, 8	Cock's-comb-shaped saccules. Gonads small.
	Dec. 19	25.5	25	5, 6, 6, 6	No saccules. No gonads.
Beach near mouth of Malampaya River, Palawan Island, 2 specimens.	Dec. 26	75	83	8, 8, 8, 8	Cock's-comb-shaped saccules. Gonads small.
Ulugan Bay, Palawan Island, near mouth of Baheli River, 6 specimens.	Dec. 28	......	......	......	All small. Caught in seines.
San Miguel Bay, east coast of Luzon, 8 specimens.	1909 June 14	76	74	7, 7, 7, 7	Immature. Cock's-comb-shaped saccules.
		81	89	7, 7, 5, 5	Do.
		73	80	5, 7, 4, lost.	Do.
Bolinao Bay, west coast of Luzon, seine 130 feet, 13 specimens.	May 10	69	76	6, 7, 7, 7 Largest specimen.	Cock's-comb-shaped saccules well developed. Immature gonads very small. Height of sensory niche above margin 11.5 mm.
		22	26	6, 6, 6, 5 Smallest specimen.	No gastric saccules and no gonads. Bell more transparent than in adult. Sensory niche 3 mm. above margin.

Genus PERIPHYLLA Steenstrup, 1837.

Periphylla, Steenstrup, 1837, Acta et Cat. Mus. Hafniensis.—Mayer, 1910, Medusæ of the World, vol. 3, p. 543.—Browne, 1910, National Antarctic Expedition, vol. 5, Medusæ, p. 42.

GENERIC CHARACTERS.

Coronatæ with 4 interradial rhopalia and 12 tentacles, 4 perradial and 8 adradial. 16 marginal lappets grouped into 4 pairs of rhopalar and 4 pairs of tentacular lappets. A deep annular furrow separates the dome-like apex of the exumbrella from marginal zone of bell. Between this ring-furrow and the lappets is a zone of 16 pedalia, 12 in the tentacular and 4 in the rhopalar radii, and these are separated one from another by 16 deep, radiating clefts, which extend down the mid-axial lines of the lappets. There are 4 deep, interradial subgenital pits in the floor of the subumbrella, lined above their edges by rows of internal gastric cirri. The large central stomach extends peripherally outward into the subumbrella in the 4 perradii. These 4 openings lead into a wide ring-sinus in the subumbrella, which in turn sends out a radiating vessel in the radius of each tentacle and rhopalium, 16 in all. These vessels fork before reaching the tentacles or rhopalia, and their diverging ends curve around the edges of the lappets and form a marginal ring-canal.

I believe that *Periphylla hyacinthina* can not be separated specifically from *P. dodecabostrycha.* The shape of the bell is quite variable, and when large the medusa usually becomes relatively flat and dome-like, whereas it is relatively high and conical when young. *P. hyacinthina* is said to be densely pigmented with purple-brown so that the gonads can not be seen through the bell walls, whereas *P. dodecabostrycha* is said to be less densely colored and semi-translucent. This distinction does not always apply and certainly the degree of pigmentation appears to be quite independent of the shape of the bell, whether flat and dome-like or high and pointed. Browne (1910), in his study of the Scyphomedusæ of the Atlantic National Expedition, concludes that *P. dodecabostrycha* is probably only a large-growth phase of *P. hyacinthina,* and with this opinion I am heartily in accord.

Periphylla hyacinthina Steenstrup.

The *Albatross* obtained 21 specimens of this common deep-sea medusa among the Philippine Islands, between depths of 338 and 1,291 fathoms, as follows:

Station.	Date.	Depth.	Character of bottom.	Size and number of specimens.	Variety.
D 5201 and D 5203 off Limasaua Island.	1908 Apr. 10	*Fathoms.* 554 to 775	Gray sand and mud, and green mud.	2 large 190 mm. wide, 105 high.	Dodecabostrycha.
D 5373, near Marinduque Island, about 15 miles off shore.	1909 Mar. 2	338	Soft sand.......	2 large.........	Dodecabostrycha.
D 5379, about 37 miles off Mompog Island, near Marinduque Island.	Mar. 4	920	....	4 medium......	Dodecabostrycha.
D 5471, from about 15 miles off Point Light, east coast of Luzon.	Mar. 19	568	....	....	Hyacinthina.
D 5486, from 6 miles off Batobobo Point, Panaon Island.	July 31	585	....	7 large and medium.	Dodecabostrycha.
D 5497, about 10 miles off Bantigui Island.	Aug. 3	960	Green mud and fine sand.	1 large.........	Dodecabostrycha.
D 5507, off northern Mindanao.	Aug. 5	425	Green mud and fine sand.	2 medium......	Dodecabostrycha.
D 5628, Pariente Strait, about 7 miles from St. Lamo Island.	Nov. 30	1,291	Gray mud......	1 medium......	Hyacinthina.
D 5647, Buton Strait....	Dec. 16	519	Green mud.....	1 medium......	Hyacinthina.
D 5652, Gulf of Boni.....	Dec. 17	525	....	1 medium......	Hyacinthina.

Genus LINUCHE Eschscholtz, 1829.

Linuche, ESCHSCHOLTZ, 1829, Syst. der Acalephen, p. 91.

GENERIC CHARACTERS.

Coronatæ with 8 rhopalia, 4 perradial and 4 interradial. 8 tentacles, 16 marginal lappets. With hernia-like sacs of the gastrovascular cavity protruding from the floor of the subumbrella. 8 gonads grouped in 4 pairs close to the 4 perradii. The central stomach opens by 4 perradial ostia into a ring-sinus which in turn breaks up into 16 branching, radiating pouches in the lappets. A marginal ring-canal is present in the Pacific *L. aquila,* and according to Vanhöffen also in *L. unguiculata* of the Atlantic.

Linuche unguiculata var. aquila.

Linerges aquila, Haeckel, 1880, Syst. der Medusen, p. 496.
Linuche aquila, Mayer, 1910, Medusæ of the World, vol. 3, p. 560, figs. 356 B and C.
Linuche unguiculata, Vanhöffen, 1913, Zoologischen Jahrbüchern, Suppl. 11, Heft 3, p. 429.

This variety is widely distributed over the tropical Pacific and is closely related to the tropical Atlantic *L. unguiculata*, with which it is identical in form and dimensions, being about 13 mm. high and 16 mm. wide. It has 48 wart-like protuberances upon the subumbrella arranged in 2 rows instead of in 3, as is commonly the case in the Atlantic medusa. 8 of the subumbrella sacs in the variety *aquila* alternate with the gonads and 8 arise from the sides of the gonads themselves. Thus in the Pacific medusa we have two zones of protuberances, an inner zone of 16 large sacs, and an outer of 32 small subumbrella saccules. The 16 large sacs lie in the mid-regions of the gonads, while the 32 small saccules lie at the zone of the outer ends of the gonads. In the Atlantic form, the areas of brown cells are commonly developed only centrifugal to the zone of gonads, while in the Pacific variety they occur *between* the gonads as well as beyond them. A marginal ring-canal is present. The Pacific variety is, however, found also in the Atlantic.

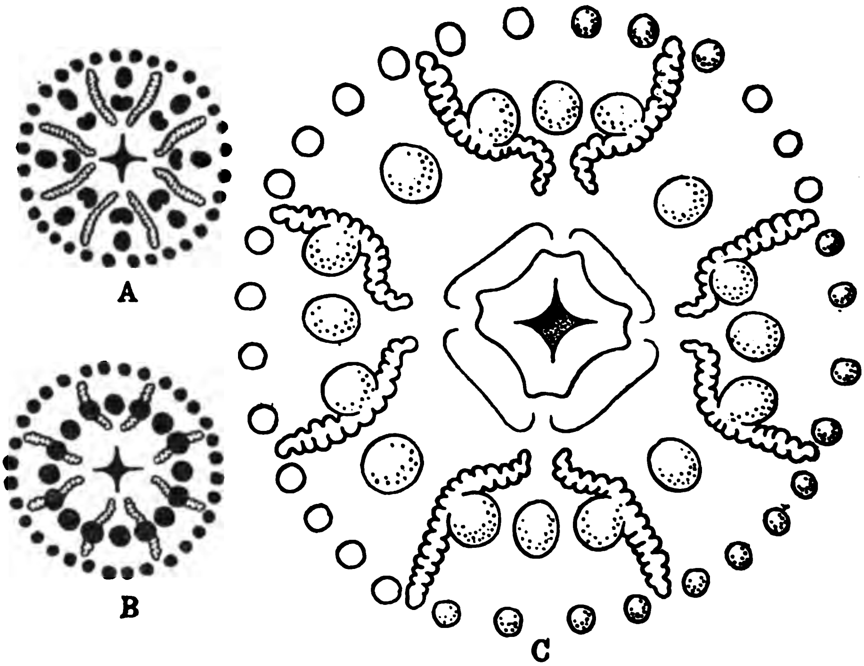

Fig. 1.—A. Showing usual arrangement of subumbrella warts in *Linuche unguiculata* of the tropical Atlantic.
B. Showing arrangement of subumbrella warts of the variety *aquila* of the tropical Pacific.
C. Enlarged view of central portion of the subumbrella of the variety *aquila*, showing lips, gonads, and saccules.

Vast swarms of these medusæ are found among the atolls of the Fiji and Paumotos Islands, and they extend to the coasts of Africa and to Queensland, Australia. They abound in Queensland in the spring months, in Fiji in December, and at Singapore in April. I have studied a large collection of these medusæ taken in the Philippine Islands at Mactan, near Cebu, on April 6, 1908, by the United States Bureau of Fisheries steamer *Albatross*. All were mature.

Vanhöffen (1913) reported that he succeeded in demonstrating that a marginal ring-canal is present in the Atlantic *L. unguiculata*, although after many tests I was unable to detect its presence and am inclined to believe that the delicate membrane separating adjacent pouches was broken in Vanhöffen's specimens, which were preserved in formalin. Moreover, Vanhöffen found that in some of the Atlantic medusæ from the Bahama-Florida region the subumbrella warts are arranged as in *L. aquila* of the Pacific. It thus appears that the Pacific form is at best only a variety of the Atlantic species, and both should be called *Linuche unguiculata*.

Genus ATOLLA Haeckel, 1880 sensu Fewkes.

Atolla, Haeckel, 1880, Syst. der Medusen, p. 488.—Fewkes, 1886, Report Commissioner of Fish and Fisheries of U. S. for 1884, p. 934.—Mayer, 1910, Medusæ of the World, vol. 3, p. 561.—Browne, 1910, National Antarctic Expedition, Nat. Hist., vol. 5, Cœlenterata, V, Medusæ, p. 47.

GENERIC CHARACTERS.

Coronatæ with numerous (9 or more) tentacles and equally numerous marginal sense-organs. Twice as many marginal lappets as sense-organs. 8 adradial gonads and 4 interradial subgenital ostia. 4 lips. The tentacles and marginal sense-organs alternate regularly, but the insertions of the tentacles and their pedalia are higher up on the sides of the exumbrella than are the insertions of the pedalia of the sense-organs.

The *Albatross* collection serves to show that *A. wyvillei* and *A. bairdii* are closely related if not mere extremes of an intergrading series of one and the same species. For example, two specimens from station D 5652 in the Gulf of Boni, depth of 525 fathoms, have the margin of the central lens distinctly notched with radial furrows as in the typical *A. wyvillei;* but there is an annular ridge on the outer side of the ring-furrow with a plain peripheral margin as in *A. bairdii*. Also several other specimens show such very slight notches in the margin of the central lens that if one were not looking carefully for this feature it would surely pass unobserved and the medusa would be called *A. alexandri*. A large specimen of *A. gigantea*, from a depth of 519 fathoms in Buton Strait, shows affinities with *A. wyvillei, A. bairdii*, and *A. verrillii*. Thus the margin of its central lens is irregularly notched as in *A. wyvillei*, but without radial furrows. There is an annular ridge upon the outer side of the ring-furrow, and the outer edge of this ridge is simple and entire, as in *A. bairdii*, in about two-thirds of its circumference, and notched as in the typical *A. gigantea* in the remaining one-third. The central lens is more than half as wide as the medusa, as in *A. bairdii, A. verrillii*, and *A. valdiviæ*.

It is evident that intergrading conditions prevail to a hopeless degree among many of the so-called "species" of *Atolla*. In fact, I think there are but two well-distinguished species: *A. bairdii* with smooth exumbrella and *A. chuni* with well-developed and quite regularly arranged papillæ upon the exumbrella sides of the lappets. As a matter of convenience, however, we may distinguish *A. bairdii* var. *wyvillei* by the notched margin of its central lens, and the absence of a well-marked annular ridge on the outer side of its coronal furrow; for while there is often an annular ridge on the outer side of the ring furrow, the margin of the central lens usually projects over it, overarching and concealing it from view. *A. bairdii* is a case where this ridge is so well developed that it projects beyond the margin of the central lens.

35 specimens of *Atolla* were found by the *Albatross* among the Philippine Islands; and of these 18 are more or less typical *A. wyvillei*, 4 are intermediate in condition between *A. wyvillei* and *A. alexandri*, 3 are intermediate between *A. wyvillei* and *A. bairdii*, 1 combines the characters of *A. bairdii*, *A. gigantea*, and *A. verrillii*, 6 are intermediate, and 3 are *A. bairdii* forma *valdiviæ*.

The specimen of *Atolla gigantea* which shows affinities with *A. bairdii* and *A. verrillii* was dredged at Station D 5647, from Buton Strait, about 11.6 miles off North Island, depth 519 fathoms, bottom green mud. This medusa is a large one, being 130 mm. wide and with 29 tentacles. The diameter of the central lens is about 94 mm. and the thickness of its gelatinous substance 21 mm. The margin of the central lens is irregularly notched, but is without distinct radial furrows. Its margin overarches the ring-furrow, which is 15 mm. deep. The outer edge of the ring-furrow exhibits an annular ridge, which is, however, overarched and hidden under the projecting margin of the central lens. Two-thirds of the circumference of the peripheral edge of this annular ridge is entire and plain, as in *A. bairdii*, but about one-third of it is notched, the notches tending to lie in the radii of the tentacular pedalia, as in the typical *A. gigantea*.

Other dimensions of this medusa (given in millimeters) are as follows: tentacular pedalia 11.5 long, 10.5 wide; rhopalar pedalia 11.5 long, 8. 5 wide; diameter across subumbrella to outer edge of ring-muscle about 126; width of ring-muscle 7.75; diameter across zone of gonads about 96, each gonad is circular, disk shaped, and about 15 in diameter, the medusa being a female, and apparently nearly mature; diameter across central stomach about 66; length of manubrium 46.

It thus appears that in this specimen the central lens is more than half as wide as the medusa, as in *A. bairdii* and *A. verrillii*; its outer margin being slightly notched as in *A. bairdii* and *A. valdiviæ*. The annular ridge is probably concealed under the overarching edge of the central lens, as in *A. wyvillei* and *A. verrillii*. Part of the outer edge of the annular ridge is entire and even, as in *A. bairdii* and *A. valdiviæ*, and part of it is notched and furrowed, as in the typical *A. gigantea*.

It is probable that most of the so-called specific distinctions between the various Atollas are mere individual peculiarities of no greater specific value than the difference between blue eyes and brown in man.

List of stations among the Philippines from which specimens of Atollas allied to A. wyvillei were obtained.

D 5201, April 10, 1908, from Sogod Bay, Southern Leyte Island, depth 554 fathoms, bottom gray sand and mud. 1 typical *A. wyvillei* with 23 tentacles. Dimensions given in table.

D 5285, July 20, 1908, about 17.5 miles off Malavatuan Island in the China Sea, depth 272 fathoms, bottom soft mud. 11 specimens of medium size, not well preserved, but all are probably *A. wyvillei*.

D 5348, December 27, 1908, in Palawan Passage, about 33.5 miles from Point Tabonan, depth 375 fathoms, bottom coarse sand. 1 specimen too imperfect for accurate specific determination.

D 5471, June 19, 1909, about 15 miles off Sialat Point Light on the east coast of Luzon, depth 568 fathoms. 2 specimens closely allied to *A. alexandri*, one with 29 and the other with 26 tentacles. The dimensions of both are given in the table.

D 5486, July 31, 1909, about 6 miles off Batobolo Point, between Leyte and Mindanao, depth 585 fathoms. 4 badly preserved specimens, too imperfect for specific determination.

D 5493, August 2, 1909, about 5.5 miles off Diuata Point, between Leyte and Mindanao, depth 478 fathoms, bottom green mud. 4 specimens of *A. wyvillei*. The largest was 60 mm. wide, central lens 44 wide with indented margin, 22 tentacles each 21 mm. long. Another medusa was 50 mm. in diameter, central lens 29.5, with indented margin and 23 tentacles. Another medusa was 42 mm. in diameter, central lens 33 mm. wide with distinct radial furrows and notched margin, 24 tentacles. The smallest medusa was 31 mm. wide, central lens 21 mm. wide with radial furrows and notched margin, 23 tentacles.

D 5533, August 19, 1909, between Cebu and Siquijor, about 9.5 miles off Balicasag Island, depth 432 fathoms, bottom green mud and sand. 1 specimen of *A. wyvillei*.

D 5631, December 2, 1909, south of Pariente Strait, about 4.5 miles off Doworra Island, depth 809 fathoms, bottom green mud. 1 specimen approaching condition of *A. alexandri* in having no distinct indentations or furrows at the margin of the central lens. The dimensions of this specimen are stated in the table.

D 5650, December 17, 1909, in the Gulf of Boni, about 12.5 miles off Lamulu Point, depth 540 fathoms, bottom green mud. 1 specimen distorted by pressing upon the bottom of the bottle in which it was preserved, so that its specific affinities can not be determined with accuracy. The medusa was 60 mm. wide, central lens 42 mm. wide, with a few faint indentations in its margin. 24 tentacles.

D 5652, December 17, 1909, in the Gulf of Boni about 7.5 miles off Lamulu, depth 525 fathoms, bottom green mud. 4 specimens, one of which is 89 mm. wide with 31 tentacles and is an *A. wyvillei* approaching the condition of *A. alexandri*. Its dimensions are stated in the table. Another specimen has 5 furrows in the margin of its central lens, but there is a plain-edged, projecting annular ridge on outer side of ring-furrow, as in *A. bairdii*. It thus combines characters of *A. wyvillei* with those of *A. bairdii*. This medusa is 51 mm. wide and has 29 tentacles. Two other specimens, one 33 and the other 37 mm. in diameter, have each 20 tentacles, with the margins of their central lenses notched as in *A. wyvillei*, while they have well-developed annular ridges which project beyond the margin of the ring-furrow, resembling *A. bairdii* in this respect.

D 5657, December 19, 1909, in the Gulf of Boni, about 15.5 miles off Olang Point, depth 492 fathoms, bottom gray mud. 1 specimen of *A. wyvillei* 54 mm. wide, central lens 41 mm. wide, 25 tentacles.

Dimensions (in mm.) of some specimens of non-typical and typical A. wyvillei, collected by the Albatross in the Philippine Islands.

	Forma *A. wyvillei* approaching the condition of *A. alexandri*.	Typical *A. wyvillei*.	*A. wyvillei* approaching *A. alexandri*.	*A. wyvillei* approaching *A. alexandri*.	
Locality	D 5652, Dec. 17, 1909, Gulf of Boni, depth 525 fathoms, near Lamulu.	D 5201, Apr. 10, 1908, south end of Leyte Island, depth 554 fathoms.	D 5631, Dec. 2, 1909, south of Pariente Strait, depth 809 fathoms.	D 5471, June 19, 1909, off Sialet Point Light, east coast of Luzon, 568 fathoms.	
Diameter of entire medusa	89	55	68	91	44
Thickness of bell	15	26	....	19	8
Number of tentacles	31	23	23	29	26
Diameter of central lens of exumbrella.	51	40	45.5	54	25
Condition of margin of central lens of exumbrella.	Notched with about 5 more or less distinct radial furrows.	Notched with 22 radial furrows.	Only slightly wavy in places, no distinct notches.	Faintly wavy in outline, no furrows.	
Depth of coronal furrow	13	3	....	9.5	4
Length of tentacular pedalia	7	6.5	5.75	8.25	6
Width of tentacular pedalia	6.5	6	6.75	7.5	4.5
Length of rhopalar pedalia	6.5	6.5	6.75	6.25	3.5
Width of rhopalar pedalia	5	5	5.25	5.75	3
Length of marginal lappets	8	....	....		
Length of tentacles	19	13	14		
Diameter to outer edge of ring-muscle of subumbrella.	73	48	56.5	75	39
Width of subumbrella ring-muscle	5.5	3	4	4.5	2.75
Diameter across zone of gonads	47	28.5	38	50.5	25.5
Dimensions of each gonad (circumferential × radial).	....	7×5	Spherical.		
Diameter of central stomach	37	21	24	37	18
Length of manubrium	22	22	....	42	

Atolla bairdii forma valdiviæ Vanhöffen.

Atolla valdiviæ, Vanhöffen, 1902, Wissen. Ergeb. deutsch. Tiefsee Expedition, Dampfer *Valdivia*, Bd. 3, Lief. 1, p. 13, Taf. 1, Fig. 3; Taf. 6, Fign. 41–46.—Maas, 1903, Scyphomedusen der *Siboga* Expedition, Monog. 11, p. 17, Taf. 1, Fign. 3, 4; Taf. 3, Fig. 23; Taf. 12, Fig. 108.—Mayer, 1910, Medusæ of the World, vol. 3, p. 565, fig. 358.

This form is very closely related to *A. bairdii* but the central disk is only half as wide as the medusa, and the 4 septal nodes are wider than in *A. bairdii*.

The *Albatross* obtained three specimens of this medusa in the Philippine Islands on April 10, 1908, at dredging station No. 5202, in Sogod Bay, depth 502 fathoms, bottom green mud. The characters and dimensions of these specimens are given in Mayer's "Medusæ of the World," vol. 3, p. 565.

Genus PELAGIA Péron and Lesueur, 1809.

Pelagia, Péron et Lesueur, 1809, Annal. du Mus. Hist. Nat. Paris, tome 14, p. 349.

GENERIC CHARACTERS.

Semæostomata of the family Pelagidæ, in which the central stomach gives rise to 16 completely separated radiating pouches, 8 in the radii of the tentacles and 8 in the radii of the sense-organs. There are 8 adradial tentacles, 8 rhopalia, and 16 partially cleft marginal lappets. Each of the 16 stomach pouches is cleft at its distal end, where it enters the marginal lappets. There is no ring-canal.

Pelagia panopyra Péron and Lesueur.

Pelagia panopyra, Péron et Lesueur, 1807, Voyage aux terres Australes, planche 31, fig. 2.

This widely distributed tropical Pacific species is distinguished by its small, low, rounded exumbrella warts, which are elliptical in outline and have a longitudinal furrow with cross-foldings. The bell becomes about 50 mm. wide, and the œsophagus is about as long as the bell-diameter, the mouth-arms being somewhat longer. In common with the species of *Pelagia*, the color is highly variable, but the bell is usually rose-colored or violet, and the nettling-warts are violet. The gonads are usually purple and the mouth-arms violet.

There are 21 specimens of this medusa in the collection of the *Albatross* in the Philippines; 10 are from Station 5422, March 30, 1909, from a tow made at a depth of 15 feet below the surface, about 10 miles off Lusaran Point Light, between Panay and Guimaras; the largest specimen is 33 mm. wide and with large gonads, while another 28 mm. wide has only small gonads. 11 young specimens were obtained at Station D 5220, April 24, 1908, on the surface between Luzon and Marinduque at $12^h\ 57^m$ p. m. These are all small and about 10 mm. in diameter, evidently being taken from a swarm of immature individuals.

Genus CHRYSAORA Péron and Lesueur, 1809.

Chrysaora, Péron et Lesueur, 1809, Annal du Mus. Hist. Nat., Paris, tome 14, p. 364.

GENERIC CHARACTERS.

Pelagidæ with 8 marginal sense-organs, 3×8 tentacles, and typically 4×8 marginal lappets; although in *C. melanaster* the lobes may still further divide, giving 6×8 marginal lappets.

Chrysaora melanaster Brandt.

Chrysaora melanaster, BRANDT, 1838, Mém. Acad. Sci. St. Petersbourg, Sci. Nat., sér. 6, tome 4, p. 385, Taf. 16, 17

There is a well-preserved specimen of this medusa from Station D 5461, June 14, 1909, San Miguel Bay, east coast of Luzon, depth 11 fathoms. The bell is about 130 mm. in diameter and slightly flatter than a hemisphere. There are 16 radiating spoke-like streaks of faint umber color extending from near the apex of the exumbrella to the bell-margin in the radii of the 16 cleft velar lobes. These 16 streaks occupy depressed radial areas sunken below the general level of the contour of the exumbrella, and they are besprinkled coarsely with wart-like nematocyst clusters of cinnamon-brown color.

There are 8 rhopalia, 3×8 tentacles, and 6×8 marginal lobes. The velar lobes are cleft as in Brandt's figures and are nearly similar in shape and size to the ocular lappets. They are, however, not narrower at the base than outwardly, as in Brandt's figures, but are oval and taper quite regularly from base to tip.

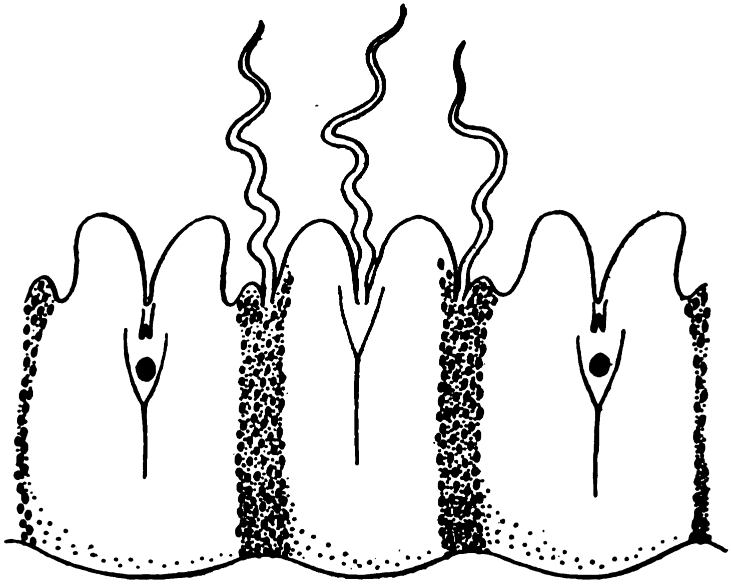

FIG. 2.—An octant of the bell-margin of *Chrysaora melanaster*, from exumbrella side.

The tentacles are short and slender, the longest being not over 60 mm.

The mouth-arms are long and slender, folded complexly, and about 170 mm. long. The gonads are well developed, apparently mature, and protrude through the subgenital ostia, the subgenital ostia being fully twice as wide as the perradial columns between them. Thus each ostium is 28 mm. long (circumferentially) and 15 mm. wide (radially), while the perradial columns of the mouth-arms are only 13 mm. wide.

In formalin the general color of the medusa is milky custard-yellow, the gonads being lighter. The apex of the exumbrella is besprinkled with cinnamon-colored nematocyst warts, and the 16 radial streaks of light umber color are also besprinkled with brown-colored clusters of nematocysts. This medusa is widely distributed over the north Pacific from Kamtschatka to California, but this Philippine Island specimen is the first which has been obtained in the tropics.

Genus DACTYLOMETRA L. Agassiz, 1862.

Dactylometra, Agassiz, L., 1862, Contributions to Nat. Hist. U. S., vol. 4, p. 166.

GENERIC CHARACTERS.

Pelagidæ with 8 rhopalia. 5×8 tentacles and 6×8 marginal lappets.

Dactylometra africana Vanhöffen.

Dactylometra africana, Vanhöffen, 1902, Wissen. Ergeb. deutsch. Tiefsee Expedition, Dampfer *Valdivia*, Bd. 3, Lief. 1, p. 40, Taf. 4, Fig. 20.

Disk 100 to 130 mm. wide with exumbrella thickly covered with wart-like clusters of nettling cells. 6 well-developed marginal lappets and 5 long tentacles in each octant. Lappets and tentacles red. Red radial streaks over exumbrella. Œsophagus, palps, and gonads not highly colored. Colors of large specimens duller and more brownish than those of small medusæ and not unlike the coloration of *D. quinquecirrha*. Distinguished by its lappets being deeply pigmented near the margin on the exumbrella side.

Vanhöffen's specimens came from the Great Fish Bay, coast of German Southwest Africa, in October 1898. Five specimens, all imperfect, the largest about 105 mm. in diameter and with only 3×8 tentacles and 4×8 marginal lappets, were found by the *Albatross* at Station D 5461, June 14, 1909, at a depth of 12 fathoms, about 7.2 miles off Corregidor Light, Manila Bay, Luzon. The bells are pinkish in hue, and thickly and uniformly besprinkled over the exumbrella with red-brown nematocyst warts. The lappets are edged on the exumbrella side with reddish brown. The tentacles have been lost and the mouth parts are imperfect.

Another specimen, 166 mm. in diameter and with mouth-arms 280 mm. long, was found at Kowloon, China, on August 14, 1908. It has 3×8 tentacles, and 6×8 marginal lappets, the lappets being edged on their exumbrella margins with russet brown.

Light (1914, Philippine Journal of Science, vol. 9, p. 198) records a *Dactylometra* from the Philippines which he believes is identical with *D. quinquecirrha*. The bell is white, translucent, and covered on the exumbrella with minute white spots.

Light's specimens were all in the *Chrysaora* stage with 24 tentacles and 32 marginal lappets. The sting which this medusa inflicts is far more severe than that given by the *Dactylometra* of our American coast.

Genus SANDERIA Goette, 1886.

Sanderia, Goette, 1886, Sitzungsber. Akad. Wissen. Berlin, Jahrg. 1886, p. 835.—Vanhöffen, 1902, Wissen. Ergeb. deutsch. Tiefsee Expedition, Dampfer *Valdivia*, Bd. 3, Lief. 1, p. 37.

GENERIC CHARACTERS.

Pelagidæ with 16 marginal sense-organs, 16 tentacles, and 32 cleft marginal lappets. 4 lips, 4 interradial gonads, and 32 peripheral stomach-pouches in the radii of the tentacles and sense-organs. No marginal ring-canal.

Sanderia malayensis Goette.

Sanderia malayensis, Goette, 1886, Sitzungsber. Akad. Wissen. Berlin, Jahrg., 1886, p. 835.—Vanhöffen, 1902, Wissen. Ergeb. deutsch. Tiefsee Expedition, Dampfer *Valdivia*, Bd. 3 Lief. 1, p. 38, Taf. 3, Fig. 12; Taf. 8, Figs. 69–74.—Mayer, 1910, Medusæ of the World, vol. 3, p. 590.

Found in the Indian Ocean, Gulf of Aden, at Singapore, and off the east coast of Africa. Some specimens of this medusa were found by the U. S. Fisheries Bureau steamer *Albatross* in the Philippine Islands between March and June 1908.

A perfect specimen, found by the *Albatross* on March 8, 1908, at Station D 5175, in the Sulu Sea, southeast of Cagayanes Islands, Philippine Islands, had a bell 75 mm. wide, palps 46 long, central stomach 35 wide, contracted tentacles 65 long, and with 25 to 30 finger-shaped projections upon each gonad.

One large imperfect specimen about 97 mm. in diameter is from Station D 5291, July 23, 1908, depth of 173 fathoms, about 2.2 miles off Escarceo Light, Southern Luzon. Only 3 gonads are left. These have between 14 to 26 papillæ.

Eight other specimens, of medium size are from Station D 5386, March 9, 1909. Depth 287 fathoms, about 25.3 miles off Arena Point, Ragay Gulf, Luzon.

One imperfect specimen is from Station D 5532, August 13, 1909, from between Masbate and Leyte. Bell about 73 mm. wide and with 26 to 29 finger-shaped processes on the gonads.

One perfect specimen is from Station D 5456, June 7, 1909, East coast of Luzon, about 6.7 miles off Legaspi Light.

Genus DISCOMEDUSA Claus, 1877.

Discomedusa, CLAUS, 1877, Denkschrift, Wien Acad., Bd. 38, p. 42.
Ulmaris + *Umbrosa*, HAECKEL, 1880, Syst. der Medusen, p. 545.
Umbrosa, MAAS, 1908, Expédition Antarctique Française, Meduses, p. 9.

GENERIC CHARACTERS.

Ulmaridæ with 24 (3×8) tentacles, 32 (4×8) lappets, and 8 sense-organs. The tentacles arise from the clefts between the marginal lappets. There are 8 simple, unbranched, adradial canals, 8 branched, perradial, and interradial canals, and a marginal ring-canal.

Discomedusa philippina Mayer.

Discomedusa philippina, MAYER, 1910, Medusæ of the World, vol. 3, p. 607, fig. 388.

This medusa bears a close resemblance to *Parumbrosa polylobata* Kishinouye (1910, Journal College of Science, Tokyo, Japan, vol. 27, Art. 9, p. 19, plate 4, figs. 20–23); but in Kishinouye's medusa the marginal lobes are still further divided, being 64 instead of 32 as in *D. philippina*. Moreover, the canal-system appears to be less complex in its branching in *P. polylobata*, so that it seems probable that the two are distinct species, not mere growth-stages one of the other. Should this view prove erroneous, however, the medusa should be called *Parumbrosa polylobata* Kishinouye.

Genus AURELLIA Péron and Lesueur, 1809.

Aurellia, PÉRON ET LESUEUR, 1809, Annal. du Mus. Hist. Nat., Paris, tome 14, p. 357.
Aurelia, LAMARCK, 1817, Syst. Anim. sans Vertebrés, tome 2, p. 512.
Aurellia, MAYER, 1910, Medusæ of the World, vol. 3, p. 619.

GENERIC CHARACTERS.

Semæostomata with a simple central mouth-opening which is surrounded by 4 well-developed, perradially situated, unbranched mouth-arms or palps. 8 marginal sense-organs. The tentacles are small and alternate with an equal number of short lappets. Both tentacles and lappets arise from the sides of the exumbrella a short distance above bell-margin. The bell-margin is divided into 8 or 16 broad velar lobes. The central stomach gives rise to a number of branched, radiating canals which anastomose and are connected by a marginal ring-canal. There are 4 interradial gonads and 4 well-developed subgenital pits.

Aurellia aurita (Linnæus).

Medusa aurita, Linnæus, 1758, Systema Naturæ, ed. 10, tomus 1, p. 660.
Aurellia flavidula, Péron et Lesueur, 1809 Annal. du Mus. Hist. Nat., Paris, tome p. 14, 369.
Aurelia aurita, Lamarck, 1817 Hist. Anim. sans Vert., tome 2, p. 513.

13 specimens of this universally distributed medusa were found by the *Albatross* among the Philippine Islands. 11 half-grown specimens are from station D 5663, December 28, 1909, in Macassar Strait, depth 11 fathoms, about 1.7 miles off Kapoposang Island, $7^h\ 20^m$ p. m. 2 larger but still immature from Station D 5662, December 21, 1909, Flóres Sea, near Tana Keke Island, $5^h\ 40^m$ to $6^h\ 12^m$ a. m.

Aurellia labiata Chamisso and Eysenhardt

Aurelia labiata, Chamisso und Eysenhardt, 1820, Nova Acta Phys. med. Leop. Car., tome 10, p. 358, planche 28, figs. 1 A. B.—Mayer, 1910, Medusæ of the World, vol. 3, p. 628, fig. 398.—Light, 1914, Philippine Journal of Science, vol. 9, p. 200.

Light, 1914, records a specimen of this medusa from the Philippines the bell of which was 225 mm. in diameter, 107 mm. across the gonads, and with each mouth-arm 100 mm. long.

Aurellia labiata is distinguished from *A. aurita* by having 16 notches in its bell-margin, by its peculiar velum-like, inter-rhopalar, subumbrella membranes representing the true bell-margin, and by the very small size of its subgenital ostia. The mouth-arms are also shorter than one commonly observes them to be in *A. aurita*, and the terminal branches of the radial-canals anastomose to a greater degree than in *A. aurita*.

The dimensions of three specimens obtained by the United States Fisheries Bureau steamer *Albatross* at Masbate Anchorage, Philippine Islands, on April 21, 1908, are as follows:

	mm.	mm.	mm.
Diameter of umbrella	174	189	128
Diameter across zone of gonads	57	53	42
Length of each mouth-arm	74	75	52

Four other specimens were caught at night upon the surface under the electric light, at Jolo Anchorage, on February 8, 1908.

An abnormal but perfect specimen of *Aurellia aurita* was found at Tortugas, Florida, on July 27, 1914. This aberration closely resembled the normal *A. labiata* of the Pacific. There were 16 deep notches in the bell-margin, 8 perradial and 8 interradial, and the velum-like marginal membrane was like that of *A. labiata*. The small subgenital ostia and simple mouth-arms also recalled *A. labiata*, but the terminal branches of the adradial-canal system did not anastomose and in this resembled *A. aurita* rather than *A. labiata*. The case is interesting, as it leads one to suspect that *A. labiata* of the Pacific has been derived as a mutation from the universally distributed *A. aurita*. The bell of this Tortugas medusa was 270 mm. in diameter. Diameter of genital cross 78 mm. Palps simple and each about one-eighth longer than the bell-radius. 8 sense organs, 8 interradial notches in the bell-margin. 8 straight, simple, *non-pigmented* perradial-canals, 8 straight pink-colored interradial-canals. The sparingly branched adradial-canals reach the bell-margin without anastomosing and in this respect resemble those of *A. aurita*. The male gonads were pink, the tentacles rich purple, the velarium creamy white, the palps purple-pink, and the gelatinous substance pink.

Genus CASSIOPEA Péron and Lesueur, 1809.

Cassiopea, Péron et Lesueur, 1809, Annal. du Mus. Hist. Nat. Paris, tome 14, genre 24, p. 356.

GENERIC CHARACTERS.

Rhizostomata pinnata with 8 (4 pairs of) adradial, complexly branched mouth-arms, the lower or ventral surfaces of which bear numerous mouth-openings and vesicles. There are 4 gonads and 4 separate subgenital cavities. There are more than 8 marginal sense-organs and twice as many radial-canals as sense-organs. The radial-canals are placed in communication one with another by means of an anastomosing network of vessels. A well-defined ring-canal may or may not be present, but is commonly absent.

Cassiopea andromeda var. baduensis, nov. var.

Medusa andromeda, Forskål, 1775, Descript. que in Itinere Orientali Observavit, Hauniæ, p. 107, tab. 31.
Cassiopea andromeda, Eschscholtz, 1829, Syst. der Acalephen, p. 43.

A specimen of this medusa is from Endeavour Strait between Australia and New Guinea, and was found by the *Albatross* on December 23, 1908. The bell is 101 mm. in diameter, flat without an aboral depression, and with 18 rhopalia. There are 4 to 8 usually 6 lappets between successive rhopalia. The arm-disk is octagonal, 36 mm. wide, and the 8 mouth-arms are each 34 mm. long and definitely *bifurcated*, the forks being 16 mm. long, thus nearly half as long as the total length of the mouth-arms. There are no appendages among the mouth-arms, but these may have been lost. The color has wholly faded in formalin.

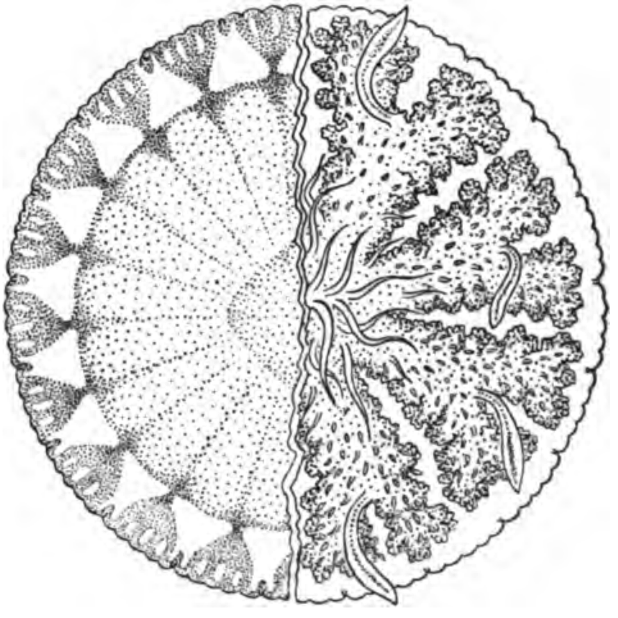

Fig. 3.—*Cassiopea andromeda* var. *baduensis*. Aboral view of half of the exumbrella on the left. Oral view of 4 of the mouth-arms on the right.

Another specimen of this medusa was found at Badu Island, Torres Straits, Australia, within a few miles of Endeavour Strait, by the Expedition of the Carnegie Institution of Washington, on November 5, 1913, and was studied alive.

The bell is 61 mm. in diameter. There are 22 marginal sense-organs and (5×22) 110 bluntly rounded, barely perceptible, evenly spaced marginal lappets all similar each to each. The arm-disk is about one-third as wide as the bell-diameter and the mouth-arms are compressed dorso-ventrally and when fully expanded extend slightly beyond the bell-margin, but in their ordinary state of contraction they do not quite reach the bell-margin. The side branches of these mouth-arms are short, but each arm is bifurcated at its outer end, the forked part being about one-third as long as the entire arm. There are about 20 slender, flat, tapering, central arm-disk appendages of various lengths, the longest of which is at the center of the oral side and is about half as long as the bell-radius. There is also a spatula-shaped appendage at the crotch of bifurcation of each mouth-arm. These are somewhat stouter than the central appendages, about half as long as the bell-radius, and with a bluish entoderm. There are numerous, minute, spatulate appendages among the mouth-arms.

The general color of the bell of the medusa is olive-brown. There are 22 large, triangular white spots with forked outer ends near the bell-margin in the radii of the sense-organs, and also (3×22) 66 short white streaks near the margin in the radii of the velar lappets. There are 22 interradial, dull bluish streaks in the subumbrella alternating with the rhopalia in position.

This variety is distinguished by its bifurcated mouth-arms. Its nearest ally appears to be *Cassiopea andromeda* var. *acycloblia* Schultze, from Amboina, but it differs in its color pattern, in the absence of a central dome, and in its simple bifurcated mouth-arms, those of the Amboina medusa branching dichotomously.

Cassiopea andromeda is the common species of the Indian Ocean, Red Sea, and Malay Archipelago, and Kellar records its having wandered into the Suez Canal. It gives rise to numerous local varieties.

There are evidently a number of other varieties of *Cassiopea* in the Philippines, for Light (1914, Philippine Journal of Science, vol. 9, p. 201) describes *Cassiopea polypoides* var. *culionensis*, *C. polypoides?*, and *C. medusa*, nov. sp. The last named is distinguished by its very large mouth-arm appendages which, in a medusa whose bell is 260 mm. in diameter, are 110 mm. long and 7.5 mm. in diameter, being cylindrical near the base and flattened at their outer ends. *C. medusa* is described from Culion Bay, Culion, Philippine Islands.

Genus CEPHEA Péron and Lesueur, 1809.

Cephea, Péron et Lesueur, 1809, Annal. du Mus. Hist. Nat., Paris, tome 14, p. 360.

GENERIC CHARACTERS.

Rhizostomata dichotoma in which the 8 mouth-arms fork once dichotomously and each fork gives rise to short dichotomous or dendritic branches. Solid, wart-shaped tubercles at the center of the exumbrella. The central stomach gives rise to 8 rhopalar and numerous inter-rhopalar radial-canals, all of which connect with a network of anastomosing vessels in a wide zone near the margin. Rhopalia without ocelli and without sensory pits on the exumbrella. There is no definite ring-canal. Development unknown.

Cephea octostyla (Forskål).

Medusa octostyla, Forskål, 1775, Descript. Anim. Itin. Orient., p. 106, No. 18, Icon., tab. 29.
Cephea octostyla, Mayer, 1910, Medusæ of the World, vol. 3, p. 652, fig. 405.

Many well-preserved specimens of *Cephea octostyla* were obtained by the United States Fisheries Bureau steamer *Albatross* at Jolo Anchorage, Philippine Islands, tropical Pacific, in February and March 1908, and have been described in Mayer's "Medusæ of the World," vol. 3, p. 652.

Cephea cephea var. cœrulea, non typical.

Cephea cærulea, VANHÖFFEN, 1902, Wissen. Ergeb. deutsch. Tiefsee Expedition, *Valdivia*, Bd. 3, Lief. 1, p. 45, Taf. 4, Figs. 13, 14.—MAYER, 1910, Medusæ of the World, vol. 3, p. 657.

One well-preserved specimen of this medusa was found by the *Albatross* at Station D 5457, June 8, 1909, 5 miles off Legaspi Light, east coast of Luzon.

The bell is flat, 109 mm. wide, with a low dome-like apex 34 mm. wide which is completely covered with long, conical, wart-shaped protuberances. There are 2 small ocular and 8 completely fused velar lappets in each octant, forming mere exumbrella thickenings on the exumbrella side of the bell-wall, and bridged over on the subumbrella side by a web of tissue. The arm-disk is 50 mm. wide and the mouth-arms are laterally flattened, 29 mm. wide in the radial direction, and 44 mm. long. There are 3 to 6 slender filaments among the mouths of each mouth-arm. These taper to pointed ends and the longest are only 13 mm. long. There are no filaments upon the central parts of the arm-disk, but there are some at the bases of the mouth-arms. The filaments are thus much smaller and less numerous than in Vanhöffen's *C. cærulea* from the east coast of Africa.

There are 8 rhopalar radial-canals which extend straight to the sense-organs, and in addition there are from 5 to 7 inter-rhopalar canals in each octant, which anastomose and lose their identity in a wide network of vessels which send branches to the rhopalar canals. The subgenital porticus is unitary. A color note states that the mouth-arms were pale hyaline blue and raw umber in color.

Cephea, sp.

Five specimens of *Cephea*, too poorly preserved to be determined specifically, were collected at the following stations:

April 25, 1909, from Manila Bay, surface.
April 29, 1909, from Manila Bay, behind the breakwater.
D 5452, June 7, 1909, off Legaspi Island, east coast of Luzon.
D 5453, June 7, 1909, off Legaspi Island, east coast of Luzon.
D 5461, June 14, 1909, Carino Island, east coast of Luzon.
Light (1914) records *Cephea cephea* from Manila Bay in January 1912.

Genus COTYLORHIZA L. Agassiz, 1862.

Cotylorhiza, AGASSIZ, L., 1862, Cont. Nat. Hist. U. S., vol. 4, p. 152.

GENERIC CHARACTERS.

Rhizostomata dichotoma with 8 simple, bifurcated mouth-arms, the terminal branches of which branch pinnately. The 4 subgenital ostia are simple and funnel-shaped, and there is a single subgenital porticus. The appendages upon the mouth-arms are mounted upon pedunculated filaments. There are 8 marginal sense-organs and numerous radial-canals which anastomose laterally without any definite ring-canal in the adult. The sense-clubs have no ocelli and no exumbrella sensory pit. There is a unitary peripheral zone of circular muscles and an inner zone of radial-muscles in the subumbrella. The exumbrella is smooth and without an aboral "sucker-like" depression, but with a prominent central dome without wart-shaped elevations upon it.

Cotylorhiza pacifica, sp. nov.

A single specimen of this interesting medusa was obtained at the launch landing in Manila Bay, Luzon, Philippine Islands, on January 24, 1908. Unfortunately it was cut into several pieces before being preserved and this renders an attempt to study it unsatisfactory in many respects. The bell appears to have been about 200 mm. wide, exumbrella finely granular, with a central dome as in *Cotylorhiza tuberculata*.

There are 8 rhopalia without ocelli (in formalin), and without exumbrella pits, being similar in essential respects to those of *Cotylorhiza tuberculata*. The rhopalar lappets are short and pointed. There are about 8 irregularly spaced, bluntly pointed, large velar lappets in each octant, and deep furrows between them extend radially inward over the exumbrella, as in *C. tuberculata*. The velar lappets vary in length, but the largest are about twice as long and twice as wide as the ocular lappets.

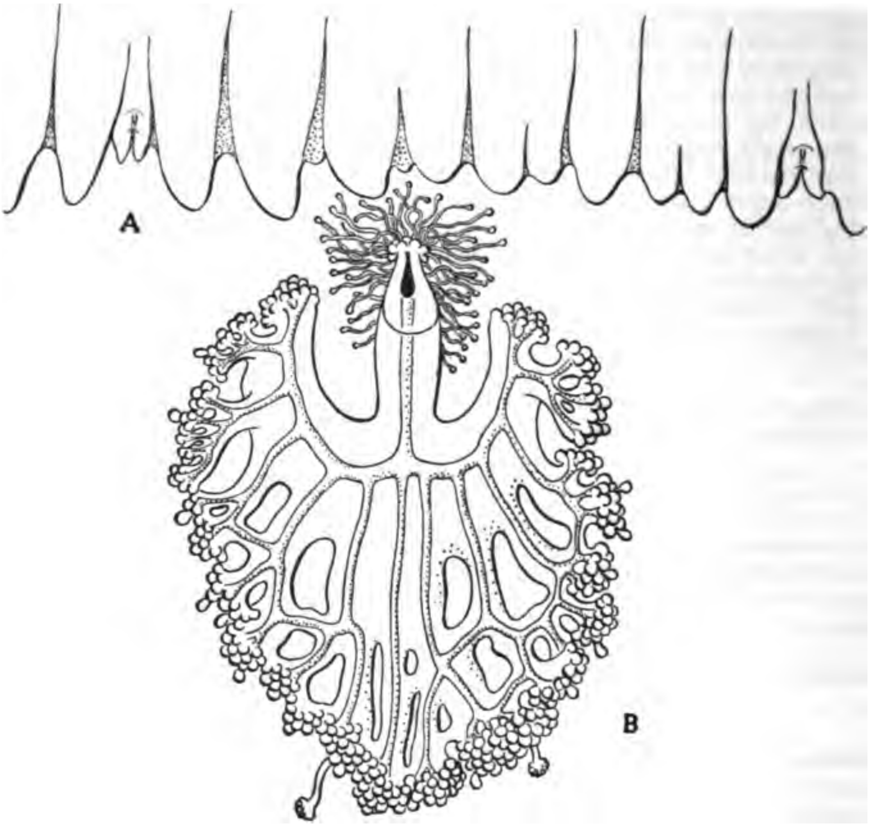

FIG. 4.—*Cotylorhiza pacifica*, sp. nov.
A. View of an octant of the bell-margin seen from the exumbrella side.
B. Abaxial view of one of the mouth-arms.

The circular muscles occupy the entire zone of the subumbrella beyond the arm-disk. They are broken in the 8 principal radii, and unlike *C. tuberculata* there are no radial muscles.

The arm-disk is about 100 mm. wide, the perradial columns being each 36 mm. wide. The subgenital ostia are much larger than in *C. tuberculata*, but they were so mutilated that one can not state their exact size, which appears, however, to be nearly that of the perradial columns themselves. The specimen having been cut into pieces, we can make no statement concerning the condition of the subgenital porticus.

The 8 mouth-arms resemble those of *C. tuberculata*, but there are window-like openings in the lateral membranes, as in *Lobonema smithii*. The total length of each arm is 81 mm., the upper arm being one-fourth as long as the lower arm. At their widest part the arms are about three-fourths as wide as they are long. The center of the arm disk is thickly covered with slender filamentous appendages which terminate in nematocyst-bearing, swollen, knob-like ends, as do the appendages of the mouth-arms of *C. tuberculata*. In this Philippine Island medusa the appendages of the outer parts of the mouth-arms are much less numerous and smaller than in *C. tuberculata*, but are similar in general form to those of the Mediterranean medusa. The longest are about 15 to 20 mm. long.

The cruciform central stomach gives rise to about 140 radial-canals, the 8 rhopalar canals being about twice as wide as the others, instead of being of the same calibre, as in *C. tuberculata*. All these canals anastomose in a network under the zone of the circular muscles. There is no distinct ring-canal. In formalin the specimen is dull uniform yellowish-brown.

It differs from *Cotylorhiza tuberculata* in having no radial-muscles, and in the circular muscles being interrupted in the 8 principal radii. The subgenital ostia and arm-disk are larger and the appendages of the mouth-arms smaller and fewer than in *C. tuberculata*. Moreover, the peculiar window-like openings in its mouth-arm membranes at once distinguish this species.

These distinctions are indeed of such a nature that if one felt so inclined a new genus could be established to receive this medusa. I believe, however, that its relationships will be more clearly indicated by placing it in the genus *Cotylorhiza*, within which it forms a well-marked species.

Genus CATOSTYLUS L. Agassiz, 1862.

Catostylus (in part), Agassiz, L., 1862, Cont. Nat. Hist. U. S., vol. 4, pp. 152, 153.

GENERIC CHARACTERS.

Rhizostomata triptera, in which the mouth-arms bear neither clubs, filaments, nor other appendages. 16 radial-canals, 8 rhopalar, and 8 adradial. The rhopalar-canals extend to the bell-margin, but the adradial-canals end in the ring-canal. On both its inner and outer sides the ring-canal gives off anastomosing vessels which may join with the radial-canals, but which do not connect directly with the central stomach. Among characters of minor importance, the marginal zone of circular muscles in the subumbrella is only partially interrupted in the 8 principal radii. There is an exumbrella pit with radiating furrows above each sense-organ.

Catostylus purpurus Mayer.

Catostylus purpurus, Mayer, 1910, Medusæ of the World, vol. 3, p. 671, fig. 412.—Light, 1914, Philippine Journ. of Science, vol. 9, p. 207.

This form is closely related to *Catostylus stiphropterus*, from Ternate, but differs in the number and arrangement of its marginal lappets, and in its deep, uniform purple-brown color. Light (1914) describes this medusa from life, whereas Mayer had only preserved material. In life the bell is higher than a hemisphere, whereas in its contracted state in preservative fluids it is flatter than a hemisphere. When mature it is deep purplish brown, and the sense-organs have brilliant silver ocellus-like spots which are larger in small than in full-grown medusæ. When young the medusa may be plum-colored, or even translucent white. Small cyclops-like crustacea were found by Light to be commensal with this medusa, the crustaceans lying upon the rhopalar canals close to the sense-organs.

Light finds that Mayer is mistaken respecting the habits of this medusa and that it is not a bottom form, but swims in shallow water near the surface.

Seven specimens found in Manila Bay on December 9, 1907, are in the collection made by the United States Fisheries Bureau steamer *Albatross*, and a larger one found on March 11, 1908. This largest specimen serves as the type of the species in the National Museum at Washington. Its dimensions in millimeters are as follows: Bell 115 wide, evenly rounded, 35 high; arm-disk 75 wide where it arises from the subumbrella, 52 wide at level of origin of mouth-arms; mouth-arms 58 long, upper arm 7 long, lower arm 51 long and 30 wide.

Another specimen of medium size, nearly mature, was found at Cavite Anchorage, Manila Bay, Luzon, on July 2, 1909.

Light (1914) states that this is the commonest medusa in Manila Bay in November and December.

Catostylus townsendi, sp. nov.

This species is named in honor of the author's friend Dr. Charles H. Townsend, the distinguished Director of the New York Aquarium.

Six specimens were found at Station D 5594, September 30, 1909, about 6 miles off Mount Putri, Borneo, in 11 fathoms. This medusa is closely allied to *Catostylus purpurus* of Manila Bay, Philippine Islands, but in formalin its exumbrella is milky in color and bespeckled irregularly with numerous conspicuous purple-brown spots. The mouth-arms are more pointed than in *C. purpurus*. In some octants of the bell-margin the velar lappets are arranged as in *C. purpurus*, but they are usually more numerous and more irregularly arranged than in *C. purpurus*.

The dimensions of the largest specimen of *C. townsendi*, stated in millimeters, are as follows: Bell 97 wide, flatter than a hemisphere, exumbrella finely granular, gelatinous substance of a horny rigidity. Shape and consistency of the bell as in *C. purpurus*. 8 rhopalia without ocelli, in formalin, and with a deep dark-colored, furrowed, exumbrella pit.

The rhopalar lappets are small and oval, but the velar lappets are about twice as wide as long. Deep clefts between the lappets extend a short distance up the sides of the exumbrella. The velar lappets are very irregular in arrangement, although they tend to conform to that seen in *C. purpurus* of Manila Bay, Luzon, yet in most of the octants the subdivisions of the principal lappets are more pronounced and irregular than in *C. purpurus*, so that there are usually 7 or 8 main velar lappets with 10 to 14 marginal lobes in each octant.

The arm-disk is similar in shape to that of *C. purpurus*. It is 61 mm. in perradial and 45 mm. in interradial diameter. The perradial columns are 17 mm. and the subgenital ostia 20 mm. wide. The projections and papillæ of the subgenital ostia are similar to those of *C. purpurus*. The subgenital cavity is unitary.

The 8 mouth-arms are each about 64 mm. long, the upper, naked outer part of each arm being 14 mm. and the 3-winged lower part 50 mm. long. The arms are widest at the proximal parts of the 3-winged expansions which, when spread out, are about 31 wide. They taper to pointed distal ends and have no appendages among the mouth-frills.

There is a powerful unbroken zone of circular muscles in the subumbrella, 27 mm. wide, from the outer edge of the arm-disk to the bell-margin. There are also radial-muscle fibers on the abaxial sides of the 4 perradial columns of the arm disk, as in *C. purpurus*.

16 radial-canals arise from the cruciform central stomach. The 8 rhopalar-canals extend straight to the rhopalia but the 8 adradial-canals end in the

ring-canal which is beneath an annular furrow or bend in the subumbrella 13 mm. inward from the bell-margin. On its inner side the ring-canal gives rise to from 4 to 7, usually 5, centripetal canals between each successive pair of radial-canals. These centripetal vessels anastomose with one another and with the 16 radial-canals, and end blindly before reaching the stomach margin. On its outer side the ring-canal gives off a network of vessels which ramify through the lappets. In formalin the medusa is opaque milky white with irregularly clustered brown spots over the exumbrella.

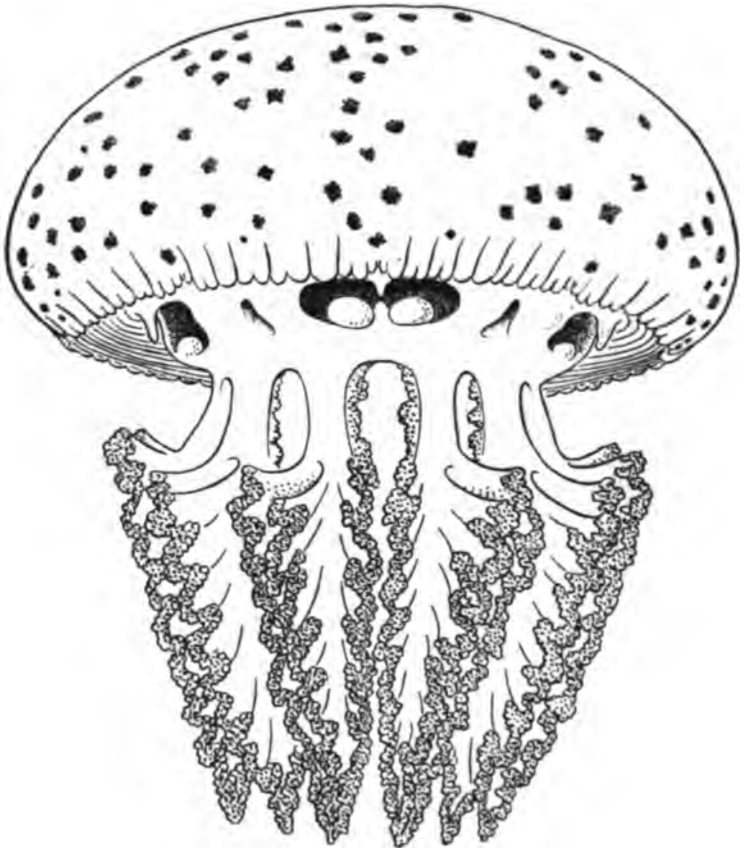

FIG. 5.—*Catostylus townsendi*, from off Mount Putri, Borneo, September 30, 1909.

This medusa is closely related to *Acromitus maculosus* Light (1914, Philippine Journal of Science, vol. 9, No. 3, sec. D, p. 212, figs. 4–6), but it has no filaments upon its mouth-arms. It is possible, however, that these were lost, but this seems improbable among 6 well-preserved specimens.

Moreover, in *Catostylus townsendi* the centripetal vessels anastomose with the 16 radial-canals, whereas in *Acromitus* they join only with the 8 rhopalar canals. It seems probable, therefore, that *Catostylus townsendi* is a distinct species separate from *Acromitus maculosus* Light, and that *Acromitus* is a genus derived from a mutation from *Catostylus*.

Catostylus mosaicus (Quoy and Gaimard).

Cephea mosaica, Quoy et Gaimard, 1824, Voyage de *l'Uranie*, Zoologie, p. 569, planche 85, fig. 3.
Catostylus mosaicus, Agassiz, 1862, Cont. Nat. Hist. U. S., vol. 4, p. 152.—Mayer, 1910, Medusæ of the World, vol. 3, p. 666.

A single immature medusa, which may possibly be the young of *C. mosaicus*, was taken by the *Albatross* in a seine off the beach near the mouth of Malampaya River, Palawan Island, Philippine Islands, on December 26, 1908. It differs from *C. mosaicus* in having only 10 marginal lappets in each octant instead of about 16, as in *C. mosaicus*. Moreover, in *C. mosaicus* the lappets are all long, pointed, and similar in size and shape each to each, whereas in the Philippine medusa there are 8 long, pointed velar and 2 much shorter, oval, ocular lappets in each octant. The Philippine medusa is, however, quite small, being only 86 mm. in diameter, whereas *C. mosaicus* becomes fully 350 mm. wide. These differences may therefore be due to immaturity. In the Philippine medusa the bell is 86 mm. wide, mouth-arms 63 mm. long, the upper arms being 11 mm. and the lower 52 mm. The interradial subgenital ostia are 18 mm. wide with a large oval or nearly spherical papilla on the subumbrella. The perradial columns of the arm-disk are only 12 mm. wide, thus the ostia are 1.5 times as wide as the columns. The perradial diameter of the arm-disk is 52 mm. and its interradial diameter 44 mm. The powerful ring-muscles of the subumbrella are only partially interrupted in the 8 chief radii. The exumbrella is coarsely granular and besprinkled thickly with numerous minute cinnamon-brown flecks. Other parts of the medusa are pale milky pink. The gelatinous substance is tough and rigid.

If this be not *C. mosaicus* it is certainly very closely related to this well-known Australian medusa. *C. mosaicus* is abundant in bays and estuaries along the Australian coast from Melbourne to the mouth of the Brisbane River in Queensland.

In Sydney Harbor all specimens of this medusa are dull creamy brown or yellowish in color, but in Moreton Bay, Queensland, most of them are cobalt blue. It is interesting to see that H. B. Bigelow (1914, University of California Publications in Zoology, vol. 13, p. 239) finds that *Stomolophus meleagris* in San Diego Bay, California, is prussian blue instead of being dull yellow, as in the Atlantic.

Catostylus mosaicus appears to breed throughout the year in Moreton Bay, Queensland, but in the temperate regions of Australia it is said to become mature only in summer and autumn.

Genus LYCHNORHIZA Haeckel, 1880.

Lychnorhiza+*Cramborhiza*, Haeckel, 1880, Syst. der Medusen, pp. 587, 633.

GENERIC CHARACTERS.

Rhizostomata triptera with filaments, but without clubs, upon the 3-winged mouth-arms. No axial terminal club at end of each arm, and no club-shaped appendages between the mouths. The stomach gives rise to 16 radial-canals: 8 rhopalar and 8 adradial. The rhopalar-canals extend to the bell-margin, but the adradial ones end in the ring-canal. Blindly ending, centripetal vessels arise from the inner side of the ring-canal and may anastomose to some extent. On its outer side the ring-canal gives off a network of anastomosing vessels which extend into the lappets.

Lychnorhiza bartschi Mayer.

Lychnorhiza bartschi, Mayer, 1910, Medusæ of the World, vol. 3, p. 674, figs. 413, 414.

Named in honor of Dr. Paul Bartsch, of the United States National Museum.

Bell 84 mm. wide, flatter than a hemisphere and with smooth exumbrella surface. Gelatinous substance thick but not very rigid. 8 rhopalia each with an ocellus, and an exumbrella sensory pit with dendritic furrows over its floor. 96 (8×12) lappets, 10 bluntly pointed velar lappets between 2 somewhat smaller ocular lappets in each octant. Arm-disk 51 mm. wide where it arises from the subumbrella, but only 47 mm. wide at the level of origin of the 8 mouth-arms. The 4 subgenital ostia are crescent-shaped and each is covered above by a gelatinous flap. They are only half as wide as the perradial columns between them. Each perradial column exhibits a niche on its outer side which bears a superficial resemblance to the subgenital ostia. The subgenital cavity is unitary.

The 8 mouth-arms are laterally compressed and 36 mm. long, the lower 3-winged parts of the arms being 24 mm. long and 23 mm. wide. Numerous simple, laterally flattened, tapering filaments arise from between the frilled mouths on all sides of the mouth-arms and from the arm-disk. The filaments upon the arm-disk are about 30 mm. long, but those from the outer parts of the mouth-arms are shorter.

The central stomach is cruciform and about 46 mm. wide. 16 simple radial-canals, 8 rhopalar and 8 adradial. These are all put into intercommunication with a wide ring-canal which is at some distance inward from the margin. The adradial-canals terminate in this ring-canal, but the rhopalar-canals extend onward to the sense-organs. On its inner side the ring-canal gives rise to 16 blindly ending networks of vessels which do not connect either with the stomach or with the radial-canals. On its outer side a fine-meshed network of vessels arises from the ring-canal and fuses with the rhopalar vessels. Around the margin at the bases of the lappets is a marginal ring-canal of fine caliber. There is a unitary uninterrupted system of ring-muscles in the marginal zone of the subumbrella, but no radial-muscles.

The gelatinous substance is translucent and milky in formalin, and the gonads, mouth-frills, and canal-system are milky yellow. Dr. Bartsch states that these colors in the living animal were nearly as they appear in the specimen preserved in formalin.

The type specimen was found by the United States Fisheries Bureau steamer, *Albatross*, at Jolo Anchorage Philippine Islands, on February 13, 1908, and 3 others were taken in Limbé Strait, Celebes, in December 1909. The dimensions given above are those of the largest specimen from the Celebes, this being somewhat larger than the type-species previously described in "Medusæ of the World," p. 674.

Lychnorhiza bornensis, sp. nov.

A single specimen of this medusa was found at Tawao, Borneo, on September 30, 1909, at 9^h 30^m a. m.

Bell 89 mm. wide, exumbrella smooth, somewhat flatter than a hemisphere. 8 rhopalia, each with an ocellus and a furrowed exumbrella pit. The rhopalar lappets are very short and lanceolate. In each octant there are usually 7, occasionally 8, velar lappets. The lappets adjacent to the rhopalar lappets are about twice as wide as the remaining velar lappets. All are oval and bluntly rounded.

The arm disk is half as wide as the bell, and the subgenital porticus is unitary. The external faces of the perradial columns have each a slight concavity, not a deep niche, as in *Lychnorhiza bartschi.* The subgenital ostia are twice as wide as the perradial columns and each is arched over by a flap-like projection. There are also 4 interradial papillæ upon the subumbrella, one opposite the opening of each subgenital ostium.

The 8 mouth-arms are not quite two-thirds as long as the bell-diameter, the upper arms being not quite half as long as the lower arms. Each mouth-arm terminates in a single, slender, tapering, thread-like filament about 50 mm. long. There are also a few shorter, more slender, filaments which arise from the sides of the mouth-arms between the mouths. There are no filaments upon the arm-disk.

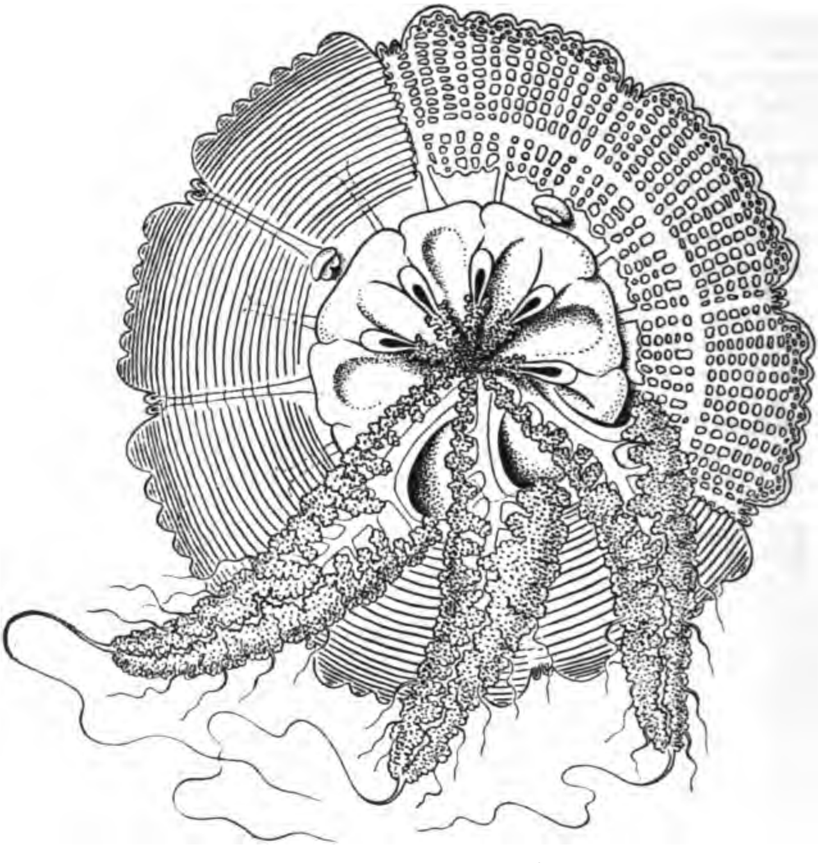

Fig. 6.—*Lychnorhiza bornensis,* from Tawao, Borneo, September 30, 1909. Natural size. The gastro-vascular canals are shown in one-third of the subumbrella. 5 arms are removed, being cut off close to the arm-disk.

There is a wide zone of circular muscles in the subumbrella, and these are only partially interrupted in the 8 rhopalar radii.

The central stomach gives rise to 16 radial-canals, 8 of which extend to the rhopalia and the 8 others end in the ring-canal. On its inner side the ring-canal gives rise to 16×4 radial-vessels, which do not reach the margin of the stomach but anastomose one with another and with the 16 chief radial-canals. On its outer side the ring-canal gives rise to about 100 radiating vessels all of which anastomose by side branches, forming a reticulum in the outer zone of the subumbrella.

In formalin the gelatinous substance is translucent and milky and the gonads and mouth-frills are milky yellow.

The following table will serve to indicate the distinctions between *Lychnorhiza bornensis* and *Lychnorhiza bartschi* of the Philippines:

	L. bartschi.	*L. bornensis.*
Velar lappets	(8×12) all oval and similar each to each.	(8×7) those adjacent to rhopalar lappets being twice as wide as the others.
Interradial papillæ on the subumbrella.	None	4.
Perradial niches in the arm-disk.	4 deep clefts	4 wide, shallow grooves.
Mouth-arms	Less than half as long as bell-diameter.	About two-thirds as long as bell-diameter.
Filaments	Numerous. Lateral filaments as long as those at outer tips of mouth-arms. Longest filaments are upon arm-disk.	A single slender filament at outer end of each arm. Other arm-filaments are very short and slender. No filaments upon arm-disk.
Circular muscles	Entire	Almost interrupted in 8 principal radii.
Canal system	Network on inner side of ring-canal does not fuse with the 16 radial-canals.	Network on inner side of ring-canal fuses with 16 radial-canals.
Central stomach	Narrow and cruciform	Wide and cruciform.

Genus MASTIGIAS L. Agassiz, 1862.

Mastigias, AGASSIZ, L., 1862, Cont. Nat. Hist. U. S., vol. 4, p. 152.

GENERIC CHARACTERS.

Rhizostomata triptera with 3-winged mouth-arms, which terminate in a naked, club-shaped extremity. There are also smaller clubs and filaments between the frilled mouths. The mouths are developed not only along the edges of the 3 leaf-like wings of the lower parts of the mouth-arms, but also over parts of their flat, expanded sides. The central stomach gives rise to 8 rhopalar-canals and numerous, interocular radial-canals, all of which anastomose and finally connect with the ring-canal. The rhopalar-canals extend straight to the sense-clubs, but the inter-rhopalar-canals end in the ring-canal. On its outer side the ring-canal gives off a network of vessels which extend into the lappet-zone and fuse with the outer ends of the rhopalar-canals. The ring-muscles of the subumbrella are interrupted in the 8 rhopalar radii. There is a unitary subgenital porticus.

Mastigias papua (Lesson).

Cephea papua, LESSON, 1829, Voyage de la *Coquille*, Zooph., p. 122, planche 11, figs. 2, 3.

Mastigias papua, AGASSIZ, L., 1862, Cont. Nat. Hist. U. S., vol. 4, p. 152.—MAYER, 1910, Medusæ of the World, vol. 3, p. 678, fig. 415.—LIGHT, 1914, Philippine Journ. of Science, vol. 9, p. 209.

This common medusa is widely distributed over the Malay Archipelago, Indian Ocean, and China Sea to Japan, and outward over the Pacific to the Fiji Islands. It gives rise to a number of varieties. Eight specimens, the largest 59 mm. in diameter, were found by the *Albatross* in the Philippines. Two specimens are from Santiago River, Pagapas Bay, Luzon, February 20, 1909; two are from Pandanon Island between Cebu and Bohol, March 24, 1909, and four were taken on the surface off Cebu on September 5, 1909. It was abundant in shallow water among the mangroves in Port Moresby, Papua, in November 1913.

Mastigias ocellata (Modeer).

Medusa ocellata, Modeer, 1791, Nova. Acta. Phys. Med., N. C., tome 8, Append., p. 27.
Cephea ocellata, Péron et Lesueur, 1809, Annal. du Mus. Hist. Nat. Paris, tome 14, p. 361.
Mastigias ocellata, Haeckel, 1880, Syst. der Medusen, p. 623.—Mayer, 1910, Medusæ of the World, vol. 3, p. 680.

The *Albatross* found small medusæ of this variety in March and April, and a mature one in January in the Philippines, in 1908. It is distributed over the eastern parts of the Indian Ocean and in the China Sea.

Genus PHYLLORHIZA L. Agassiz, 1862.

Phyllorhiza, Agassiz, L., 1862, Cont. Nat. Hist. U. S., vol. 4, p. 158.

GENERIC CHARACTERS.

Similar to the closely allied *Lychnorhiza*, but the centripetal vessels which arise from the inner side of the ring-canal join with the central stomach, as in *Mastigias*, instead of ending blindly as in *Lychnorhiza*. The canal-system resembles that of *Mastigias*, but the mouth-arms have no terminal clubs.

Phyllorhiza luzoni, sp. nov.

Two specimens of this medusa were captured at a depth of 150 feet in Varadero Bay, Southern Luzon, Philippine Islands, on July 23, 1908. Unfortunately both became somewhat macerated in the preservative fluid.

The bell of the larger and more perfect specimen is 60 mm. wide, flat, and with finely granular exumbrella. 8 rhopalia without ocelli in formalin and without exumbrella pits. 16 sickle-shaped rhopalar lappets, and (9×8) 72 rounded velar lappets which are somewhat wider but not longer than the rhopalar lappets, so that the general contour of the bell-margin is circular, without deep niches in the rhopalar radii.

The arm-disk is cruciform, 32 mm. in perradial and 20 mm. in interradial diameter. The subgenital ostia are 14 mm. and the perradial columns 8 mm. wide, and the subgenital porticus is wide and unitary.

The 8 mouth-arms are slender and strongly compressed laterally, their lower parts being 3-winged with deeply incised lateral membranes. The naked outer part of each upper arm is 13 mm. and the 3-winged lower part only 11 mm. long. Any appendages which may have existed among the mouth-frills have disappeared in the preservative fluid owing to the maceration of the specimens.

The muscular system of the subumbrella consists of a broad, uninterrupted zone of weakly developed circular muscles. In other hitherto known species of *Phyllorhiza* the muscles are interrupted in the 8 principal radii.

The central stomach is cruciform, 32 mm. in perradial and 16 mm. in interradial diameter. 8 radial-canals arise from the stomach and extend straight to the 8 rhopalia and these main canals are connected one with another by a ring-canal which is 6 mm. inward from the margin of the bell. In each octant 6 to 9 radiating vessels arise from the cruciform stomach anastomosing in an irregular network with one another and with the 8 main canals. On its outer side the ring-canal gives rise to a fine-meshed network of vessels which ramify through the lappets.

A color note states that the medusa was light green with grayish white spots.

Genus VERSURA Haeckel, 1880.

Crossostoma preoccupied for mollusks by Norris and Lycett, 1850.
Crossostoma, AGASSIZ, L., 1862, Cont. Nat. Hist. U. S., vol. 4, p. 155.
Versura+*Crossostoma*, HAECKEL, 1880, Syst. der Medusen, pp. 606, 607.

GENERIC CHARACTERS.

Rhizostomata triptera with clubs and filaments upon the mouth-arms. The 4 perradial canals arise directly from the stomach, but the 4 interradial canals result from the fusion of a number of anastomosing vessels which arise from the interradial sides of the stomach. There is no definite ring-canal, but merely a marginal network of vessels. There are no radial-muscles in the subumbrella, but the ring-muscles are well developed. Among the characters of minor importance, the subgenital ostia are wide openings, wider than the columns between them, and the sense-organs have a simple, exumbrella pit without radiating furrows. At the center of the arm-disk is a prominent, raised cluster of frilled mouths having filaments between them.

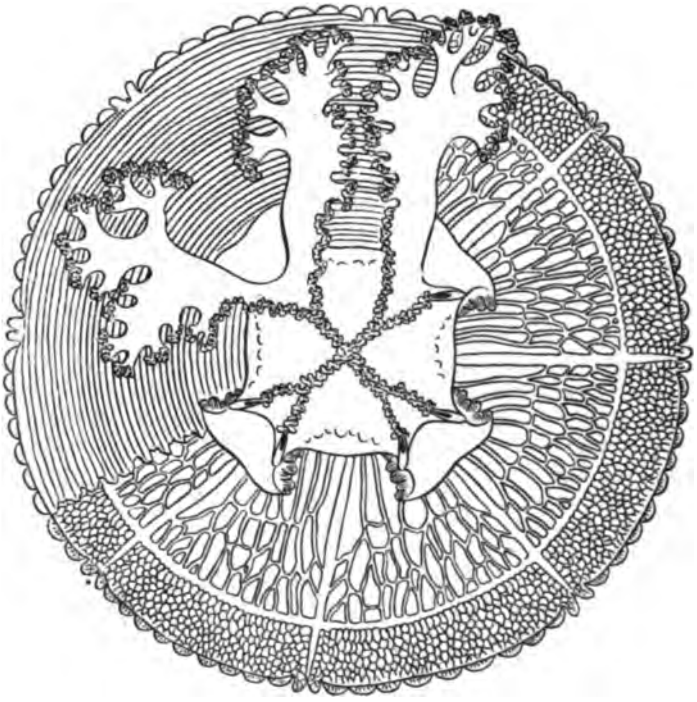

FIG. 7.—*Phyllorhiza luzoni* from Varadero Bay, Luzon. Five arms are represented as if cut off close to the arm-disk. The muscular system is shown above, and the gastro-vascular canals below

Versura maasi Mayer.

Versura maasi, MAYER, 1910, Medusæ of the World, vol. 3, p. 687, fig. 416.

Named in honor of Professor Dr. Otto Maas, in recognition of his notable researches upon medusæ. Described in Mayer's "Medusæ of the World." A single perfect specimen was obtained by the United States Fisheries Bureau steamer *Albatross* on April 8, 1908, along the shore at Mantacao Island, west coast of Bohol, Philippine Islands.

Genus LOBONEMA Mayer, 1910; sensu Light, 1914.

Lobonema, Mayer, 1910, Medusæ of the World, vol. 3, p. 688.—Light. 1914, Philippine Journ. of Science, vol. 9, p. 216.

GENERIC CHARACTERS.

Rhizostomata triptera in which the marginal lappets are greatly extended, tapering to pointed ends. These lappets are non-contractile and lack muscles. Mouth-arms with numerous filaments. Mouth-arm membranes perforated by window-like openings. 8 to 16 rhopalia and twice as many radial-canals, and a ring-canal which gives off anastomosing vessels on both its inner and outer sides. The inner network does not connect with the stomach. All of the radial-canals extend beyond the ring-canal. The subumbrella exhibits a well-developed system of ring-muscles. There are numerous, prominent, tapering papillæ upon the exumbrella. There is a sensory pit on the exumbrella side above each rhopalium, and the floor of the pit exhibits radiating, dendritic furrows.

Lobonema smithii, the first-known species and type of the genus, was obtained by the *Albatross* in Manila Bay, Philippine Islands, late in April 1908, and described in Mayer's "Medusæ of the World" (vol. 3, p. 689, figs. 417, 418). It is named in honor of Dr. Hugh M. Smith, Commissioner of Fisheries of the United States. Another species from Palawan was described by Light (1914, Philippine Journal of Science, vol. 9, p. 217, figs. 7–9) under the name *Lobonema mayeri*.

Lobonema smithii has only 8 marginal sense-organs, and the subumbrella ring muscles are entire; while in *L. mayeri* there are 12 to 16 marginal sense-organs and the circular muscles are completely interrupted in the ocular radii. Light, who studied the medusæ in life, states that the colors of *Lobonema mayeri* are an exquisite scheme of purple, violet, and rose-pink. The gonads are as a rule pink, the general color is violet, and the fringe of tapering marginal lappets purple. Dr. Light tells me that in *Lobonema smithii* these colors are not so brilliant and the bell of the medusa may be white. Light finds that the sting of this medusa is not very severe and that the cases of poisoning reported by Old were probably due to *Dactylometra* and not to *Lobonema*.

Light describes *Lobonemoides gracilis*, an immature medusa which may possibly be a young stage of *Lobonema mayeri*. The marginal lappets are pointed but are not very long, and there are no window-like openings in the mouth-arm membranes.

Genus THYSANOSTOMA L. Agassiz, 1862.

Thysanostoma, Agassiz., 1862, Cont. Nat. Hist. U. S., vol. 4, p. 153.

GENERIC CHARACTERS.

Rhizostomata lorifera having mouth-arms bearing 3 rows of frilled mouths from base to lower end, without a terminal club. Among characters of minor importance, the 4 interradial, subgenital ostia are wider than the perradial columns between them. There are 8 rhopalar canals and a ring-canal which gives off a network of vessels on both its inner and outer sides. This network connects with all the radial-canals and also at numerous points with the central stomach. The well-developed circular muscles are only partially interrupted in the 8 principal radii. There is a small, shallow, exumbrella pit above each sense-organ, and there are no furrows in the floor of the pit. The only difference between this genus and the closely allied *Lorifera* is that the frilled mouths are developed even to the tips of the lower ends of the mouth-arm and there is no terminal club, whereas *Lorifera* has a naked terminal club.

Thysanostoma thysanura Hæckel.

(?) *Rhizostoma brachyura*, Lesson, R. P., 1829, Voyage de la *Coquille*, Zoophyt., tome 2, p. 153; 1830, Centurie Zoologique, p. 227, planche 80.
Thysanostoma thysanura, Haeckel, 1880, Syst. der Medusen, p. 625, Taf. 39, Figs. 1-9.—Mayer, 1910, Medusæ of the World, vol. 3, p. 692, fig. 420.

The dimensions, in millimeters, of a specimen obtained at Mindanao, Philippine Islands, by the United States Bureau of Fisheries steamer *Albatross*, are as follows: Bell, 100 wide; perradial diameter of arm-disk, 74; diameter of arm-disk at level of origin of mouth-arms, 48; genital ostium, 40 wide; mouth-arms, 220 long, 24 wide at widest part, 12 wide at their blunt tips; 8 to 12 velar lappets in each octant; filamentary appendages on the arm-disk, 10 to 15 long; exumbrella finely granular.

In another large medusa from Mausalay, Mindoro, Philippine Islands, taken by the *Albatross* on June 4, 1908, from a depth of 150 feet, the bell is 120 mm. wide and the mouth-arms 190 mm. long. In a half-grown medusa, obtained on the surface at the same time and place, the bell is 59 mm. wide with finely granular exumbrella; mouth-arms 67 mm. long; arm-disk 41 mm. wide at its origin from the subumbrella and 33 mm. wide at the level of the origins of the mouth-arms.

Two specimens are from Atulayan Bay, east coast of Luzon, June 17, 1909. Of these the larger one was cut into two pieces when viewed by me, but the bell appears to have been about 106 mm. in diameter, the mouth-arms being 167 mm. long, the upper arm 20 mm. and the lower arm 147 mm. long.

A color note leads one to infer that in life the bell was translucent with a slightly brownish margin, and with the frilled mouths dark burnt-umber. The smaller specimen when alive had a translucent bell with some whitish spots and with 8 indigo streaks along the 8 principal radii. The frilled mouths and bell-margin were pale brown. One specimen, 91 mm. in diameter with mouth-arms 155 mm. long, is from Station D 2268, September 21, 1909, depth 13 fathoms off Singaan Island north of Tawi Tawi. In this the arm-disk is 59 mm. in perradial diameter, and the upper arms are 13 and the lower 142 mm. long.

Genus LORIFERA Haeckel, 1880.

Himanostoma, preoccupied for Diptera by Loew, 1853.
Himanostoma, Agassiz, L., 1862, Cont. Nat. Hist. U. S., vol. 4, p. 152.
Lorifera, Haeckel, 1880, Syst. der Medusen, p. 628.

GENERIC CHARACTERS.

Rhizostomata lorifera in which the 8 mouth-arms bear rows of frilled mouths throughout their lengths but terminate each in a naked knob. Among characters of minor importance the subgenital ostia are usually wider than the perradial disk-columns. The circular muscles of the subumbrella are practically entire. The sense-clubs have each an ocellus and a well-developed, exumbrella pit with radiating furrows. This genus is distinguished from the closely allied *Thysanostoma* only by the naked, club-shaped extremities of its mouth-arms.

Lorifera lorifera var. pacifica (Schultze).

Himanostoma loriferum, var. *pacifica*, Schultze, L. S., 1897, Abhandlung. Senckenberg. Naturf. Gesell., Bd. 24, Heft 2, p. 153, Taf. 15, Figs. 1, 1a, 6; 1898, Denkschrift. Med. Nat. Gesell. Jena, Bd. 8, p. 446, Taf. 34, Fig. 9 (young medusa).
Lorifera lorifera var. *pacifica*, Mayer, 1910, Medusæ of the World, vol. 3, p. 695.

A single half-grown specimen of this medusa was found at Port Palapag, Luzon, by the United States Fisheries Bureau steamer *Albatross* on June 2, 1909, being captured through the use of dynamite. Its bell is 98 mm. wide, exumbrella finely granular, flatter than a hemisphere. The bell-margin is badly damaged but there appear to be 6 to 8 cleft or subdivided velar lappets in each octant. Their general contours are rounded, and inter-lobular clefts extend radially a short distance up the exumbrella surface.

The 8 rhopalia have each an ocellus, but no exumbrella pit. Perradial diameter of arm-disk, 55 mm.; width of subgenital ostia, 34 mm.; width of perradial columns of arm-disk, 12 mm.; subgenital porticus wide and unitary; naked upper arm, 20 mm. long; length of the abaxial side of the mouth-bearing part of each arm, 35 mm.; length of the terminal naked axial filament of each arm at least 40 mm., but all are broken at their ends.

There is a thick felting of short filaments upon the arm disk.

The circular muscles are unitary, being only partially interrupted in the 8 principal radii.

The 8 radial-canals are each about 3.5 mm. wide, and in addition there are about 8×10 slender radial-canals, all of which anastomose with one another and with the 8 chief radial-canals, forming a wide network in the subumbrella.

In formalin the 8 chief radial-canals are violet.

Schultze describes this medusa from Ternate and from Amboina, Malay Archipelago.

PART II.

HYDROMEDUSÆ OF TORRES STRAITS, AUSTRALIA.

DESCRIPTION OF SPECIES.

Genus STOMOTOCA L. Agassiz, 1862.

Stomotoca, AGASSIZ, L., 1862, Cont. Nat. Hist. U. S., vol. 4, p. 347.—MAYER, 1910, Medusæ of the World, vol. 1, p. 108

GENERIC CHARACTERS.

Stomotocini with 2 long diametrically opposed perradial tentacles with hollow basal-bulbs. With or without other smaller tentacles or cirri, and with or without abaxial, ectodermal ocelli at the bases of the tentacles or cirri. The interradial or adradial gonads are complexly folded and may migrate outwards more or less along the 4 radial-canals. These radial-canals are broad and flat and there is a well-developed circular canal. The hydroid appears to be *Perigonimus*.

Stomotoca turrida (Mayer).

(Plate 1, Fig. 1.)

Dissonema turrida, MAYER, 1900, Mem. Mus. Comparative Zool. at Harvard Coll., vol. 37, p. 44, plate 2; also, 1910, Medusæ of the World, pp. 116, 490, plate 10, fig. 1; plate 22, fig. 1.
Amphinema turrida, BIGELOW, H. B., 1909, Mem. Mus. Comparative Zool. at Harvard College, vol. 37, p. 200, plates 7, 40, 43, and 44.

This medusa was fairly common at the Murray Islands, Torres Straits, Queensland, Australia, late in September 1913. H. B. Bigelow found it in Acapulco Harbor, Pacific coast of Mexico, and it is common at Tortugas, Florida. The largest of the Murray Island specimens was still immature, the bell being only 4 mm. in height, whereas at Tortugas, Florida, the bells of mature medusæ are usually about 6 mm. high. It differs from the Tortugas medusæ in its duller color, the green being absent, and there are no ocelli on the abaxial sides of the 2 main tentacles. The marginal cirri are only beginning to develop and the adradial gonads are beginning to migrate outward along the radial-canals. The absence of ocelli at the bases of the 2 long tentacles may be due to the immaturity of the specimen, for they are sometimes absent from the tentacle bases of small medusæ at Tortugas, Florida. Altogether the differences between the tropical Pacific and the tropical Atlantic medusæ appear to be too slight to warrant their specific separation. This species is closely related to *Stomotoca octædra*, but differs in having numerous marginal cirri each with an abaxial, ectodermal, basal ocellus.

Genus CYTÆIS Eschscholtz, 1829.

Cytæis, ESCHSCHOLTZ, 1829, System der Acalephen, p. 104.

GENERIC CHARACTERS.

Cytæidæ with 4 simple, radially placed, marginal tentacles, and with 4 or more simple, unbranched, oral tentacles.

Cytæis atlantica (Steenstrup).

(Plate 1, Fig. 2.)

A single specimen of an immature *Cytæis* was found at the Murray Islands, Torres Straits, Australia, on September 27, 1913. There were 8 simple oral tentacles and the manubrium was mounted upon a small peduncle, this being an indication of immaturity. The bell was half-egg-shaped, 3.5 mm. high with thin walls. 4 perradial marginal tentacles, each about two-thirds as long as the bell-diameter, and with large swollen basal bulbs, each with an abaxial ectodermal ocellus and a mass of dark brown entodermal pigment. The manubrium is about two-thirds as long as the depth of the bell-cavity and the ectoderm is brownish yellow with a deeply pigmented, brown, central region. The 4 radial-canals and the ring-canal are narrow and uniform in width.

This form so closely approaches the typical *C. atlantica* of the Mediterranean and tropical Atlantic that I believe the two to be identical.

Genus LAODICIA Lesson, 1843.

Laodicia, Lesson, 1843, Hist. Zooph. Acal., p. 294.

GENERIC CHARACTERS.

Thaumantiadæ with 4 gonads upon the 4 radial-canals. Clubs and cirri may arise from or near the bell-margin between the tentacles. Ocelli may occur on the inner (centrad) sides of the tentacle bulbs. The stomach lacks a peduncle and has 4 simple lips. The gonads extend outward from the sides of the stomach along the radial-canals and in mature medusæ they nearly touch the ring-canal. The hydroid is *Cuspidella* Hincks.

Laodicia fijiana A. Agassiz and Mayer.

Laodicea fijiana, Agassiz, A., and Mayer, 1899, Bull. Museum Comp. Zool. at Harvard College, vol. 32, p. 163, plate 3, figs. 9, 10.

The common Atlantic and Mediterranean *Laodicea* is *L. cruciata* L. Agassiz, which has numerous clubs and cirri between the tentacles. In the tropical Pacific this form is apparently replaced by the closely allied *L. fijiana* A. Agassiz and Mayer, which has very few clubs and wholly lacks cirri between the tentacles. Only about half of the tentacles in the Pacific form have ocelli, whereas in the Atlantic variety the majority of the tentacle bulbs bear ocelli.

Thus at Maër Island, Torres Straits, Australia, in a medusa with 120 tentacles, only 46 bore ocelli; another had 196 tentacles, only 56 of which bore ocelli. In other specimens, however, nearly three-fourths of the tentacles bore ocelli, in this respect resembling the Atlantic form.

This medusa was quite common off Maër Island, Great Barrier Reef of Queensland, in September and October. Specimens were found ranging up to 10 mm. in diameter, and in color they were milky, green, or violet as in *L. cruciata* of the Atlantic.

Genus PHIALIDIUM Leuckart, 1856.

Phialidium, Leuckart, 1856, Archiv für Naturgesch. Jahrg. 1, p. 18.

GENERIC CHARACTERS.

Eucopiidæ with 16 or more marginal tentacles some of which remain permanently rudimentary, with closed vesicular lithocysts scattered somewhat irregularly among the tentacles. 4 radial-canals upon which the 4 gonads are placed. Manubrium without a well-developed peduncle and with 4 lips. The tentacle bulbs are simple and are not flanked by cirri, and their entodermal cores do not project inward into the gelatinous substance of the bell. The hydroid is *Campanulina* Van Beneden.

Phialidium pacificum Maas.

(Plate 2, Fig. 3.)

Phialidium pacificum, MAAS, 1906, Revue Suisse de Zool., tome 14, p. 91, plate 2, fig. 7.

Specimens of this medusa were fairly common in surface tows taken off the Murray Islands, Torres Straits, Australia, in September and October. When mature the bell was flatter than a hemisphere, thin-walled, and about 4.25 to 5 mm. in diameter. In an average mature female there were 43 tentacles, all similar each to each and about half as long as the bell-radius. There were 26 small spherical lithocysts, each with a single concretion. The manubrium was small and with 4 simple lips, and the 4 swollen gonads occupied somewhat more than the middle thirds of the 4 slender radial-canals. The entoderm of the manubrium, gonads, and ring-canal was dull green to light grass-green. In some medusæ the entodermal lamella of the bell was green, but in others it was transparent and colorless.

A comparison between the figures of this medusa from Torres Straits and one from the Mediterranean shown in figure 143, page 268 of Mayer's "Medusæ of the World," will show that the two are identical in all essential respects. Moreover, it will be recalled that Calkins (1899, Proc. Boston Soc. Nat. Hist., vol. 28, p. 349) described a hydroid from Puget Sound, Pacific coast of North America, which appears to be identical with the hydroid of *Phialidium hemisphæricum* of the Atlantic, and Murbach and Shearer record a medusa from Puget Sound which may be derived from this hydroid. In fact were our Murray Island medusa found in the Mediterranean or off the coasts of Europe, we would at once call it *Phialidium hemisphæricum*; if off the American coast, *P. languidum*, and if in the Tropical Pacific, *P. pacificum*. These names merely express the doubt that still exists respecting the specific identity of the hydroids of these medusæ, for no differences can be detected between the mature medusæ themselves.

When young, this Torres Straits medusa passes through a stage wherein there are 16 short, equally developed tentacles, 32 lithocysts, and 4 small gonads near the ring-canal.

Genus EUTIMA McCrady, 1857.

Eutima, McCRADY, 1857, Gym. Charleston Harbor, p. 87.

GENERIC CHARACTERS.

Eucopiidæ with 8 lithocysts, 2 in each quadrant, and with 4 or more well-developed tentacles, and numerous rudimentary tentacles, marginal cirri, or both. Stomach mounted upon a well-developed gelatinous peduncle. The 4 or 8 linear gonads are developed upon the 4 radial-canals. The hydroid is *Campanopsis*.

Eutima australis nov. sp.

(Plate 3, Fig. 5.)

This medusa was common in surface tows off the Murray Islands, Torres Straits, Australia, in September and October 1913. The bell is flatter than a hemisphere and the gelatinous substance is thin and tenuous. There are 4 perradial tentacles each about as long as the bell-radius and with laterally flattened, hollow, basal bulbs which are not flanked by cirri. The basal bulbs extend upward over the exumbrella in the manner described by Browne for *Eutima curva.* There are about 64 short, blunt excretory papillæ upon the bell-margin and about one-quarter of these are flanked by one or occasionally two short coiled cirri. A dense black pigment collects in these excretory papillæ but is discharged if the medusa be left for several days in an aquarium without food. There are 8 adradial lithocysts, each with 7 to 9 spherical concretions. The gelatinous peduncle is about 1.25 times as long as the bell-diameter, and is conical above, and slender, 4-sided, and prismatic below. The stomach is about one-fifth as long as the peduncle, and there are 4 recurved and complexly crumpled lips. The 8 gonads are developed upon those parts of the radial-canals which lie over the subumbrella and the peduncle, but appear to reach maturity only over the peduncle. The gonads, stomach, and tentacle bulbs are dull milky in color, all other parts being transparent.

The nearest ally of this medusa is *Eutima elephas* of the North Sea and Tropical Atlantic, but in this form there are no cirri upon the bell-margin. It is also closely related to *Eutima mira*, but the laterally flattened tentacle bulbs which extend part way up the sides of the exumbrella appear to distinguish it from this common Atlantic *Eutima.*

Genus RHOPALONEMA Gegenbaur, 1856.

Rhopalonema (in part), Gegenbaur, 1856, Zeit. für Wissen. Zool., Bd. 8, p. 245.

GENERIC CHARACTERS.

Trachymedusæ with 8 well-developed tentacles in the radii of the 8 radial-canals, and with 8 or more club-shaped or cirrus-like tentacles. All tentacles arise from the bell-margin in a single row. The 8 gonads are developed upon the 8 radial-canals. 4 lips. Stomach without a peduncle. Lithocyst clubs in inclosed cavities on the bell-margin.

Rhopalonema velatum Gegenbaur.

(Plate 2, Fig. 4.)

Rhopalonema velatum, Gegenbaur, 1856, Zeit. für Wissen. Zool., Bd. 8, p. 251, figs. 1–5.—Mayer, 1910, Medusæ of the World, vol. 2, p. 378, figs. 214–219.

Specimens of this widely distributed medusa were found off the Murray Islands, Queensland, Australia, in September and October 1913. The bell was nearly hemispherical, thin-walled, and about 8 mm. in diameter. There were 16 tentacles and 16 lithocysts following the tentacles in clockwise rotation around the edge of the bell. The linear gonads occupied the middle thirds of the 8 radial-canals. The manubrium had 4 lips, and the velum was well developed. The entodermal lamella of the bell was bottle green, all other parts being colorless.

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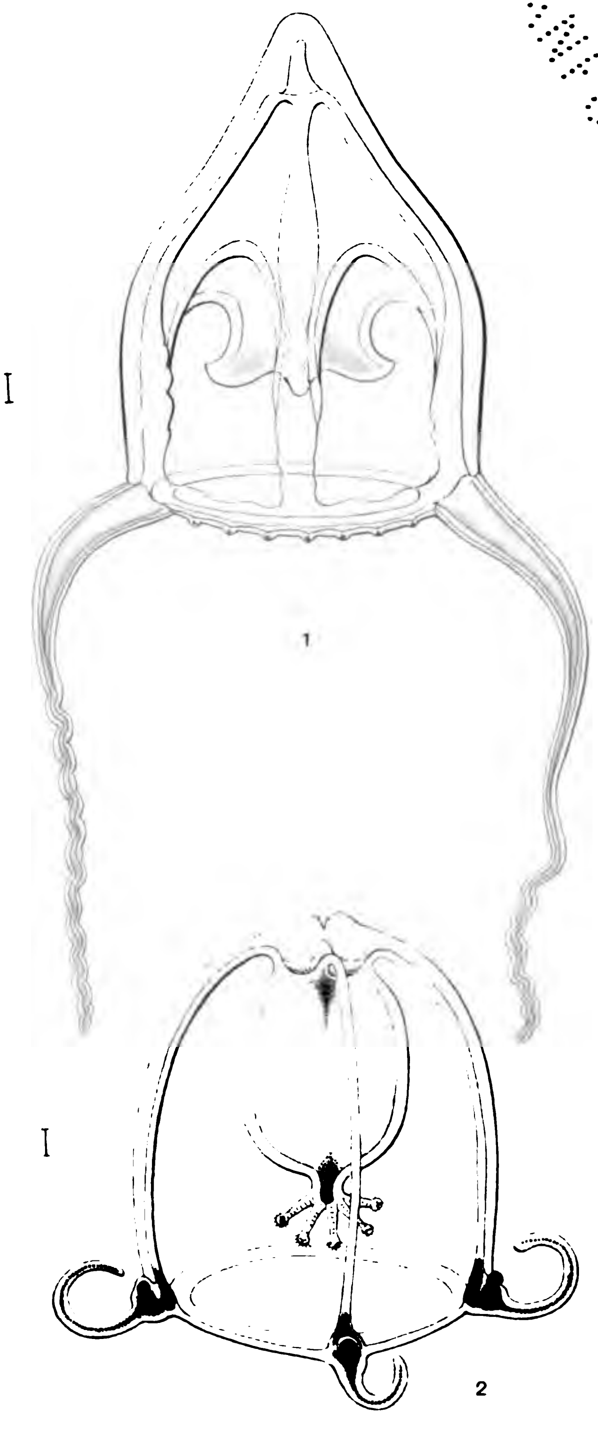
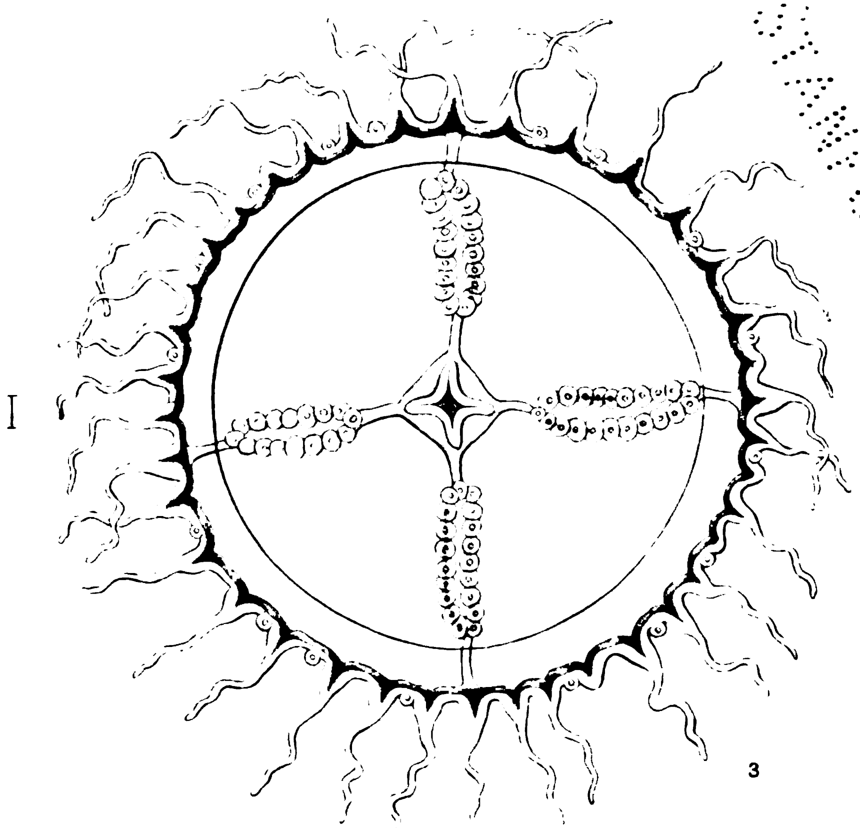


DRAWINGS FROM LIFE BY AUTHOR

A. HOEN & CO. BALTIMORE, MD.

Fig. 1. *Stomotoca turrida*, from Murray Islands, Torres Straits, September 27, 1913. Surface tow.

Fig. 2. *Cytaeis atlantica*, from Murray Islands, Torres Straits, September 27, 1913. Surface tow.



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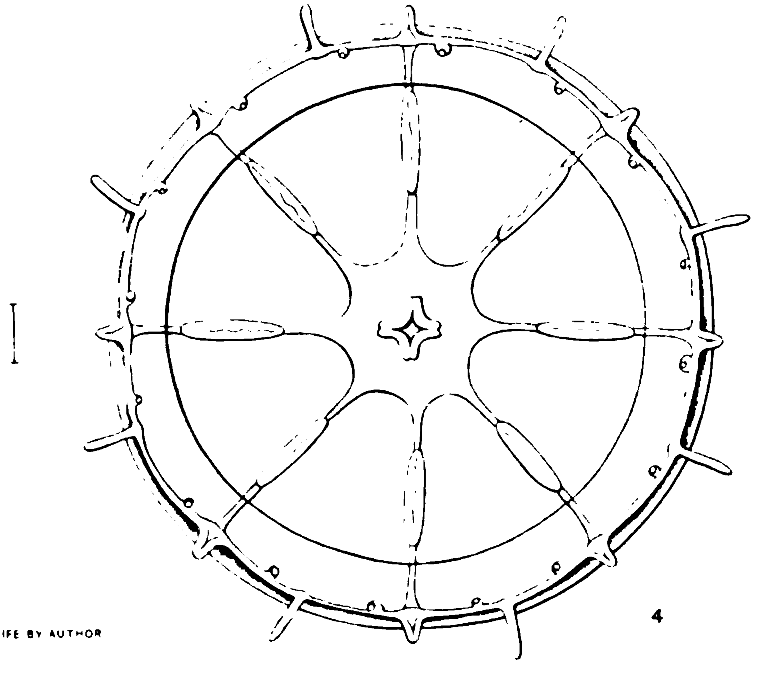

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DRAWINGS FROM LIFE BY AUTHOR

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Fig. 3. ***Phialidium pacificum*, from Murray Islands, Torres Straits, September 25, 1913. Surface tow.**

Fig. 4. ***Rhopalonema velatum*, from Murray Islands, Torres Straits, September 29, 1913. Surface tow.**

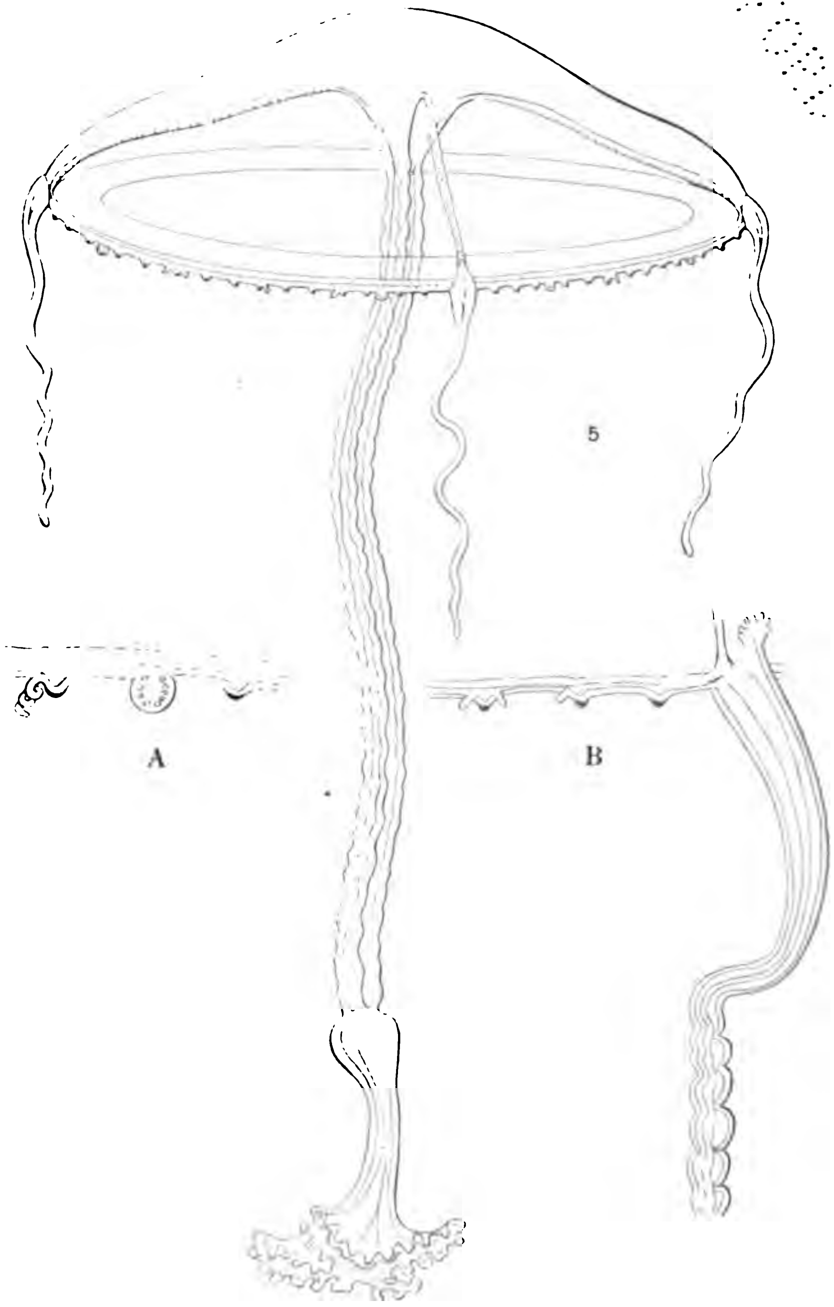

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Fig. 5. *Eutima australis*, sp. nov., from Murray Islands, Torres Straits, September 26, 1913. Surface tow. A, lithocyst; B, portion of bell-margin showing laterally flattened tentacle-bulb which extends upward above the bell-margin.

VIII.

REPORT ON THE BAHAMA CERIONS PLANTED ON THE FLORIDA KEYS.

BY PAUL BARTSCH,
Curator of Marine Invertebrates, U. S. National Museum.

Eight plates.

REPORT ON THE BAHAMA CERIONS PLANTED ON THE FLORIDA KEYS.

BY PAUL BARTSCH.

In the annual report of the Director of the Department of Marine Biology of the Carnegie Institution of Washington for 1912 (Year Book No. 11, pages 129–131), attention was called to the transplanting of a large number of two races of Bahama cerions to the Florida Keys. In Year Book No. 12 (1913) of the same Institution, a report of the results of the planting of Bahama cerions on the Florida Keys was made, on pages 169–172. In 1914 these plantations were visited at the end of April and the following results were noted. I shall first report on the conditions of the colonies in the various plantings, and then discuss the adult offspring grown in the various colonies.

April 21, 1914.—We visited the plantation which had been made in 1912, on the second Ragged Key north of Sands Key, and gathered 170 planted specimens, all but one of which were alive and seemed to be thriving; 55 of their offspring were also found, three full-grown (plate 3, the first 3 figures of the left-hand side of bottom row); the others varied in size from nepionic whorls to half-grown. We returned the original lot and two of the young to the spot, taking the 3 adults for the collection of the U. S. National Museum, at Washington. In order to isolate the generations and in the hope of starting a new colony, 50 of the young were planted in a grassy spot about 62 feet northeast from the old planting; this planting was marked with a short stake and a piece of drift bamboo was put in an old stump near the place. The members of this colony have moved but little beyond their limits of last year.

On the first Ragged Key north of Sands Key someone had built a house in the midst of our plantation. Our cerions were clinging to the walls of the house and to bushes and grass near it. We gathered 144 of the original planting, all living, and placed them near the northwest corner of the house. We also collected 50 young, which, like those found on the last key, varied from mere tips to half-grown. Not one full-grown individual produced on this key was found. We took the 50 young to Sands Key, in order to start a new colony with this generation, and planted them in the middle of the first sand stretch south of the north end, on the seaward side. The place is marked by an old skinned and bleached white tree, which forms a conspicuous landmark on the sea side. There are two lesser dead trees, one on each side of the taller. The specimens were placed in a patch of grass near the base of the outer dead tree, apparently a very favorable habitat. The distance of this key from the first Ragged Key north of Sands Key is only a few hundred yards; hence the environmental conditions are probably very nearly the same in the two places.

April 22, 1914.—Visited Tea Table Key, and found no living cerions, and only a few dead. Apparently this colony is doomed to extinction. The island is infested with crabs, being riddled with their burrows, and the small hermit crabs have probably carried off most of the shells.

On Indian Key, 20 of the dead specimens were still on the wall where we placed them last year, and 2 more were at the base where the majority were strewn. A thorough search revealed only 13 living specimens, so this colony also is on the verge of extinction. No young individuals were found in this second planting. We next visited the place where the original planting was made—the place which was so completely overrun with vegetation last year that it was deemed wise to shift the colony a little further inland. The vegetation is even more dense than last year and it was impossible to determine if any had survived here.

April 23, 1914.—In the colony on Duck Key, 107 of the marked shells were recovered, all but one alive. Many of these were copulating. We found only one young specimen, but the vegetation here is so dense that the small young could easily escape notice. The young individual obtained possessed only one postnuclear whorl. All the shells were put near the stake where we planted them last year, and it seems quite possible that this colony may survive.

The colony at Bahia Honda is doing well. We gathered 46 marked specimens—all that we could find—and took them westward to the summit of a little promontory, dropping them between the stumps of two palms and marking the place with a stake. Across the ditch from this stake stands a large palm. We did not wish them to mingle with their grown or growing offspring, which are very abundant on this plantation. We gathered 105 of the young and placed all but 13 at the base of the old stake. The 13 are full-grown, or nearly so, and these we took with us in order to compare them with the check series. (Plate 1, bottom row.) Even in the field the Florida generation appeared so remarkably different from their Bahama-born parents that we could distinguish them the moment we saw them.

On New Found Harbor Key the ground where the planting was made was swamped with a dense growth of some malvaceous plant which was overgrown with a leguminous climber. Only 11 planted specimens were found, and no young. The place was so fearfully infested with mosquitoes that a long stay and exhaustive search was impossible, but from observed facts I would say that this colony was not prospering.

The colonies at Tortugas were studied from April 25 to April 28, 1914. Of the 72 painted cerions left on Bird Key, of which only 18 were noted in 1913, none remained. On Garden Key 138 of the "King's Road Type" were planted in 1912, and of these we recovered 62, in 1913, and also one young of last year (1914), all of which we transferred to the parade ground because we believed that the conditions there would be more favorable for their existence. Someone, however, burned the grass on the inside of the fort and thus destroyed our colony. An examination of the place in 1914, where the 138 were first planted in 1912, revealed 6 living specimens of the original planting, but no young. The place was less overgrown this year than last. The cleaning up to which I subjected it last year seems to have decreased the *Ipomœa pescapræ* growth considerably, which gives the cerions a little better chance. We left the 6 specimens in this place in a bunch of grass.

On Loggerhead Key the conditions are much more favorable for the colonies, although here also we had some disappointments, for the colonies planted within the cages came to naught through an unfortunate accident.

The northern colony near the laboratory (plate 7 A), consisting of the "White House Type" cerions, was in a flourishing condition. We gathered 615 young in various stages of growth, from the mere nepionic tips to adults, and 162 of the planted specimens. The young were mostly about the bases of tufts of grass, being buried beneath the surface of the coral sand at the base of the grass bunches, from which a little scratching would bring them to the surface. The adult specimens (plate 2, top and bottom rows) of the first locally-grown generation were retained for comparison with the check series at Washington. In 100 of the larger specimens (plate 5, lower figure) we made two scratches with a file in the ribs of the upper whorls, the other 500 being left unmarked.

The 500 tips (plate 4) of the northern colony we transferred to a place 150 feet distant from and a little south of east of the stake which marked the original planting (plate 7 B). They are in the southeast corner of the same meadow in which the original planting was made, in surroundings apparently entirely similar to those in which they were born. We marked this place with a stake and a metal tag which bears the legend, "Cerions—X."

We planted the 100 marked specimens on the west side of the path between the laboratory and the light-house, about 135 feet south of the stake marking the original colony on this end of the island (plate 7 C). The planting is marked by a stake which stands in the northeast corner of the large meadow, and bears the legend "Cerions—Y." The conditions here appear to be exactly like those where the specimens were born—that is, bunches of Bahama grass and cactus forming the vegetation. This colony should therefore develop just as if the specimens had not been transferred.

The colony at the southern end of the island (plate 8 E) appears to be in equally healthy condition. We gathered 300 young specimens, some of which are figured on plate 5, upper figure, and 3 full-grown and 3 nearly full-grown individuals which were born here (plate 3, top row). The young were planted in the small meadow a little to the northeast of the one in which the original colony of the "King's Road Type" cerions were planted (plate 8 G). This new colony is on a ridge, in a scanty growth of Bahama grass, and the place is marked by a stake bearing a tag with the legend, "Cerions—Z."

The middle planting (plate 8 H), which consisted of 500 each of the "King's Road" and "White House" types, is not doing well. Part of the ground has been burned over and quite a number of the snails were destroyed. Most of the living individuals had taken to the fringe of bay cedars, and these do not appear to form a particularly suitable habitat. We cleaned the place up thoroughly, pulling up the cactus and cutting the grass, thus making an exhaustive search, which resulted in the recovery of 200 of the "White House Type" and 150 of the "King's Road Type" cerions, and a single tip. These were transferred into the second meadow northwest of the original south colony (plate 8 I). This mixed colony is marked by a stake bearing a tag with the legend, "Cerions XX." The ground here is covered by a quite regularly distributed growth of short grass.

April 29, 1914.—We visited Boca Grande and examined the colony planted about the beacon. The grass here had been burned over and most of our specimens roasted. Quite a number of young, however, were present in the tufts of grass not consumed by fire, so this colony still promises to maintain itself. Three adults and one nearly grown (plate 3, the last four figures, bottom row) of the first generation were obtained and reserved for further study.

The status of the various original plantings may therefore be briefly described as follows:

King's Road Type: Second Ragged Key north of Sands Key, good; Tea Table Key, probably extinct; Duck Key, undecided; New Found Harbor Key, almost extinct; Boca Grande Key, good; Garden Key, Tortugas, almost extinct; Loggerhead Key, Tortugas (plate 8 E), very good.

White House Type: First Ragged Key north of Sands Key, good; Indian Key, very poor; Bahia Honda, very good; Loggerhead Key, Tortugas (plate 7 A), very good.

Mixed lot: Loggerhead Key, Tortugas (Plate 8 H), as yet poor.

NEW COLONIES STARTED ON THE FLORIDA KEYS IN 1914.

1. New Importations from the Bahamas.

On June 9 the Director, at my request, planted on the Tortugas the following newly imported material from the Bahamas:

Two hundred specimens of mottled cerions, plate 6, from Spring Hill, about 6 miles east-southeast of Nassau, New Providence, each marked with two file scratches on the second from the last whorl and with two notches in the outer lip, were planted about 75 feet from the southeast corner of the main (new) laboratory building on Loggerhead Key, and the place marked with a wooden stake bearing a lead label upon which is stamped "Spring Hill, Nassau, 1914" (plate 7 D). Of this planting Dr. Mayer wrote, August 20, 1914: "I fear that all died at Tortugas, for I could find none of them on the bushes, but all lying on the ground, in July."

Five hundred of the "Kings Road Type" were marked with two file scratches on the last whorl and planted on the southern end of Loggerhead Key, S. 24° W. from the long entrance stake, and S. 80° W. from the double stake which marks the 1912 "King's Road Type" cerion planting (plate 8 F). This colony was marked by a stake bearing a lead label with the legend, "Bastian Point, Andros, 1914."

2. Transplantations of the First Generation of Florida-grown Specimens.

These new colonies, mentioned previously, are to enable us to keep track of the various generations and to observe the reaction of each to the changed environment. They are on the second Ragged Key north of Sands Key, Sands Key, Bahia Honda, and Loggerhead Key.

OBSERVATIONS ON THE ADULT SPECIMENS OF THE FIRST GENERATION OF FLORIDA-BORN INDIVIDUALS.

The largest specimens of Florida-grown cerions found last year possessed seven postnuclear whorls, which make up about half of the entire length of the shell. From the study of these young specimens, we were led to make the statement that "The results so far obtained seem to indicate that the first generation will be like the parent generation unless decided changes should take place in the later whorls, which have as yet not been developed. * * * If the present tendencies prevail in the adult shell, then we can say that the somaplasm has not at once responded to the change of environment."

The adult specimens of the first generation of both races of Florida-grown individuals now enable us to say that a decided change has taken place; that the first generation is not like the parent generation, showing that the somaplasm in both of the races of cerions subjected to experimentation has responded to the new conditions in which they were developed. The extent to which changes have taken place is well shown by the illustrations accompanying this report.

THE "WHITE HOUSE TYPE."

In order to determine the amount of variation which has taken place in the first generation of these snails born and matured in Florida, a check series (plate 1, upper row, and plate 2, middle row) of 10 specimens was selected from a lot of more than 1,000 from Andros Island, Bahamas. These were collected at the same time and place in which the specimens planted on the Florida Keys in 1912 were obtained. These 10 specimens are part of a handful which was taken at random from the box containing the lot, and the 10 specimens in turn were picked from this handful without looking at them. We therefore assume that they represent a fairly typical average series. They are characterized by quite uniform outline and sculpture.

These 10 specimens from left to right yield the data shown in table 1.

TABLE 1.—*Check series "White House Type" cerions.*

No.	No. of whorls.	Measurement of shell.	
		Altitude.	Diameter.*
		mm.	*mm.*
1	10.3	25.5	13.3
2	10.1	27	12.3
3	10.4	26.8	12.3
4	10.8	28.5	12.3
5	10.1	24.5	13
6	10.3	26.3	12
7	10.5	27	13
8	9.6	25.4	13.2
9	10.1	25.7	12.2
10	10.3	27	12.3
Average......	10.25	26.37	12.59
Greatest......	10.8	28.5	13.3
Least........	9.5	24.5	12

*This measurement in each case is the diameter of the shell from just back of the lip to a point diametrically opposite.

TABLE 2.—*First generation of "White House Type" cerions from Bahia Honda Key.*

No.	No. of whorls.	Measurement of shell.	
		Altitude.	Diameter.
		mm.	*mm.*
1†	11	31.5	13.5
2‡	11	32.8	13.4
3	10.3	29	13.3
4	10.8	29.8	13.2
5	10.7	33	13.5
6	10.5	31	14.4
7	11	30.2	13.2
8	10.4	25.5	12.1
9	10.4	24.5	13.5
10	10.6	29.8	13
Average......	10.67	29.71	13.30
Greatest......	11	32.8	14.4
Least........	10.3	24.5	12.1

†Length estimated.
‡Shell not quite adult.

A comparison of these first Florida generation shells (plate 1, lower row) with the check (Bahama parent generation) series (plate 1, upper row) shows that the general outline and sculpture seem to have been maintained, but the texture of the shells has a more glossy and harder appearance. The measurements show an increase in the number of whorls—a greater altitude with a greater range of variation. In the check series the total variation was 4 mm. In the Florida-born offspring it is 8.3 mm. The diameter has also increased materially, and with it the range of variation. In the check series this is 1.3 mm.; in the above, 2.3 mm. We may, therefore, say that the first generation from Bahia Honda, Florida, represents a much more variable organism than the parent stock in the Bahamas.

The 20 specimens of the first generation from the north colony of Loggerhead Key, Tortugas (plate 2, top and bottom rows), are extremely interesting. They possess a greater number of whorls than the check series or parent generation (plate 2, middle row). The altitude is also greater, the average of the check series being 26.37 mm.; that of the present generation, 28.80 mm. The variation in this measurement is also much increased, ranging from 25 mm. to 34 mm., as against 24.5 mm. to 28.5 mm. of the check series—*i. e.*, there is a range of 9 mm. in the present series against 4 mm. of the check series. This raises the variation in altitude 7 mm. above that observed in the first generation born and grown upon Bahia Honda, Florida. The average diameter in the north colony drops below that of the check series, being only 12.28 mm., against 12.59 mm. The range of variation, however, is much greater—*i. e.*, 11 mm. to 14.5 mm. against 12 mm. to 13.3 mm. of the check series; or 3.5 mm. against 1.3 mm. This variation exceeds even that of the Bahia Honda grown first generation, in which it was 2.3 mm.

TABLE 3.—*First generation of the "White House Type" cerions from the north colony of Loggerhead Key, Tortugas, Florida.*

[Plate 2, top and bottom rows.]

No.	No. of whorls.	Measurement of shell, in millimeters.	
		Altitude.	Diameter.
1	11.4	30.1	12.3
2	11.1	29	12
3	10.5	31.7	13.6
4	12	[1]34	12.3
5	10.6	32	14.5
6	11.3	28.1	11.7
7	11.4	31.2	13
8	11.9	31.4	12.1
9	11.6	30.2	12
10	11.5	28.1	12.3
11	11.2	*27.8	11.8
12	11.9	28.2	12.5
13	11.1	26.5	12.8
14	10.5	25	11.3
15	11.1	28	11.5
16	10.9	26.3	11
17	11.2	27.2	11.8
18	10.4	26.5	12.8
19	10.6	26	12
Average..	11.17	28.80	12.28
Greatest..	12	34	14.5
Least....	10.4	25	11

*Altitude estimated; shell not quite adult.

The shape, coloration, and sculpture have also undergone decided modification in some of the specimens. There is a pronounced tendency in the entire lot toward greater elongation. This tendency reached its maximum in the fourth and eighth specimens of the bottom line of figures, plate 2. Associated with this is the producing, attenuating, and rounding of the base, best shown in the two figures alluded to above. The sculpture in most instances follows the parent type, but in some it is decidedly different, and the variation does not follow a uniform direction.

One type of variation is shown by figure 4 of the bottom line, plate 2, in which the ribs are almost obsolete and very widely spaced. Another is represented by specimens 14, 15, and 16 of the top line, which are much darker, much narrower, and have the ribs much more crowded than the members of the check series. These two departures are so pronounced that they would probably have been considered distinct species and deemed not very closely related to the parent stock by past workers in this group unfamiliar with the history of the specimens.

THE "KING'S ROAD TYPE" OF CERIONS.

The 8 specimens figured on plate 3 were taken at random in the same way that those of the "White House Type" were selected, from a large series collected in the Bahamas. They may therefore be taken as fairly typical representations of that type. Most of the first generation produced by the colonies of this type have not yet attained the adult stage. The material at hand enables us to say that the offspring of this group show changes from the parent stock as great, if not greater, than those observed in the first generation of the "White House Type."

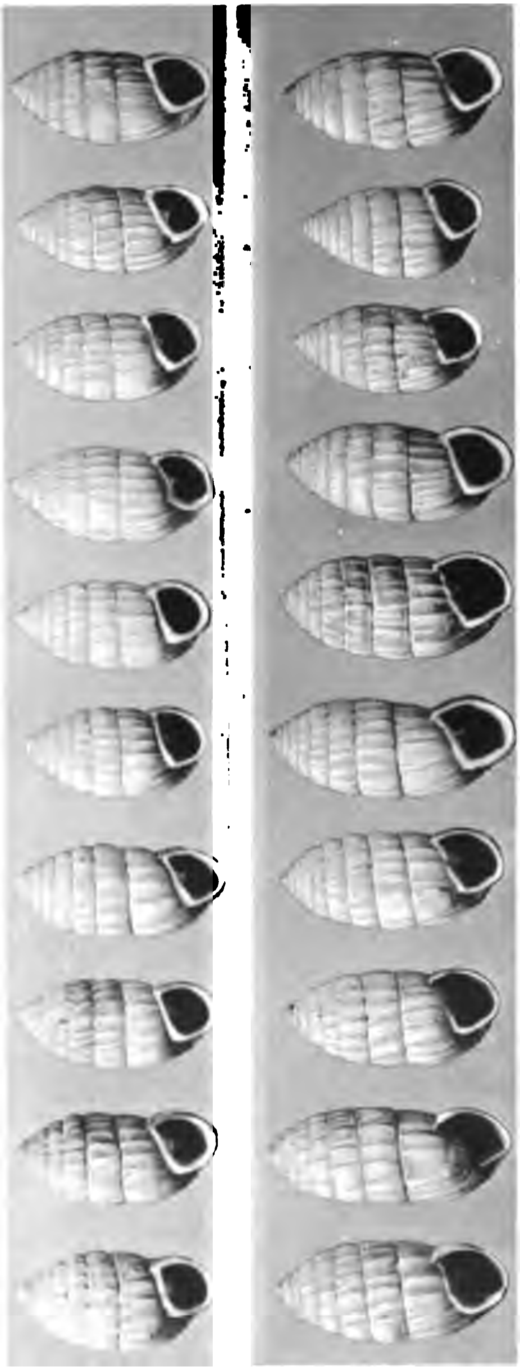
The three specimens from the second Ragged Key north of Sands Key (plate 3, figs. 1–3, bottom line) are uniformly larger, darker, and with more attenuated base than the check series.

The Boca Grande Key specimens (plate 3, figs. 4–7, bottom line) show great variation in size and also in coloration, but there is as yet not enough material to make comparisons.

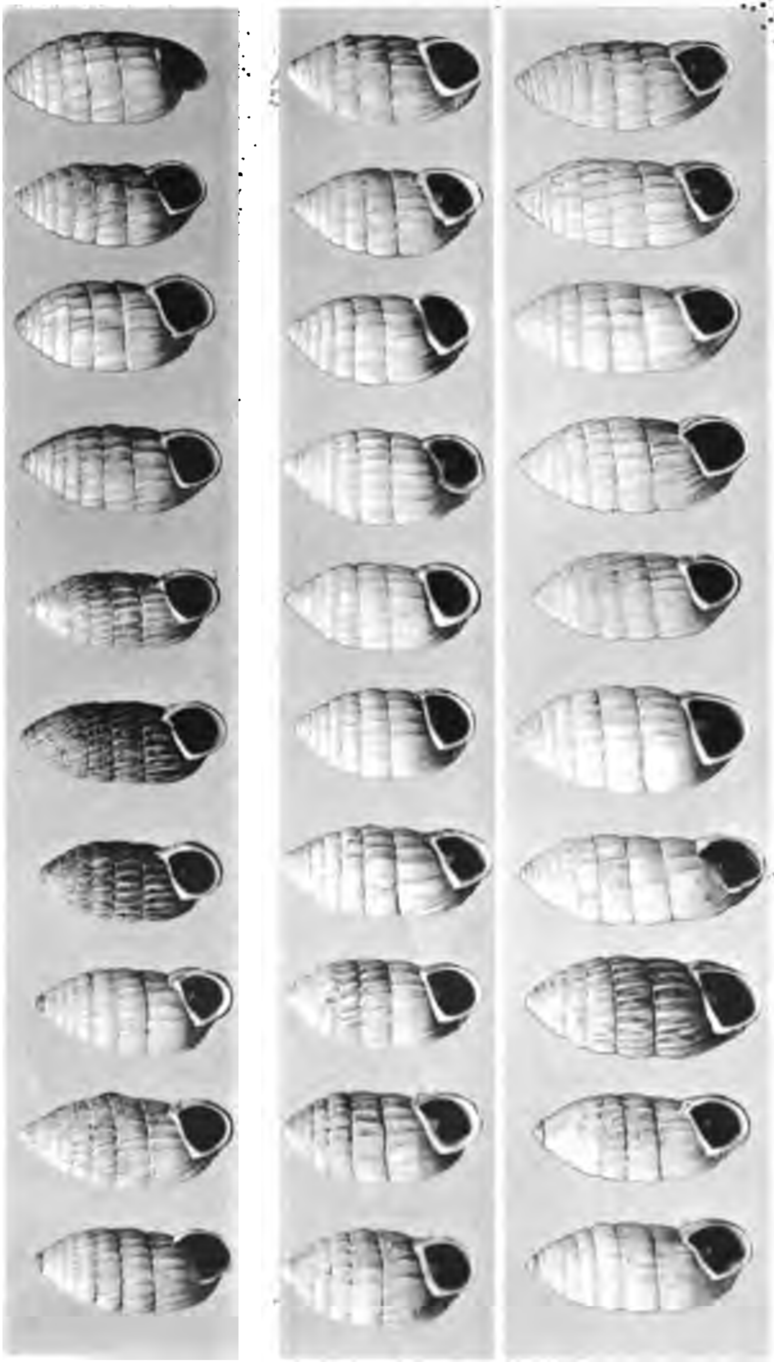
The greatest variation is shown by the first generation from the south colony on Loggerhead Key (plate 3, top row). Although only 3 specimens were found that had attained full growth, most of the others figured have attained a stage so near maturity that we can readily see that they are much larger, decidedly more attenuated, and usually darker than the check series.

It is to be hoped that next year will yield a larger series of the first generation of this type. The second generation is also looked forward to with considerable interest, since in it the germ-plasm will have been subjected to the new environment, and this may entail still greater changes than have yet been observed, *i. e.*, the effect of the new conditions upon the germ-plasm.

In the following plates all figures are natural size excepting plate 6, which is reduced about one-seventh.

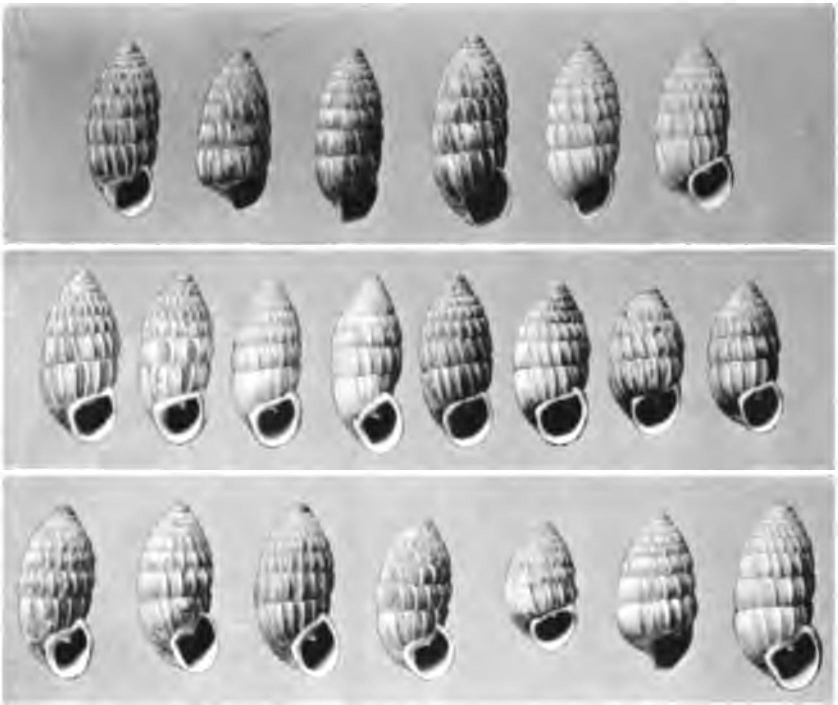


Top row of figures check series (parent generation) of the "White House type" of cerions from Andros Island, Bahamas.
Bottom row of figures first generation from Bahia Honda Key, Florida.



Middle row of figures check series of the "White House type."

Bottom row of figures 1-10, and top row 11-20, of the first generation from the North Colony of Loggerhead Key, Tortugas.



Top row of figures, first generation of the "King's Road" type from South Colony, Loggerhead Key, Tortugas.

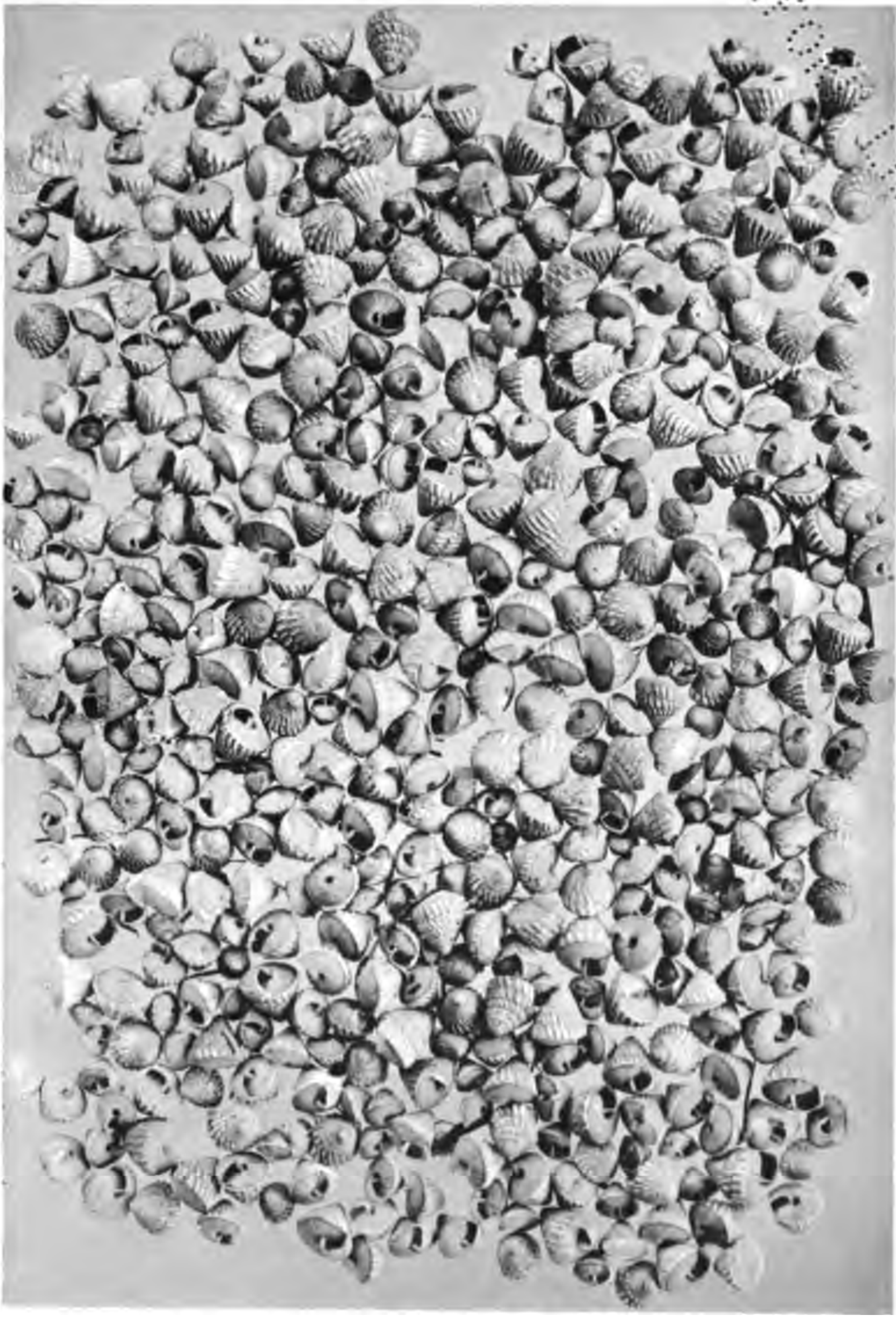
Middle row of figures, check series (parent generation) of "King's Road type" from Andros Island.

Bottom row;

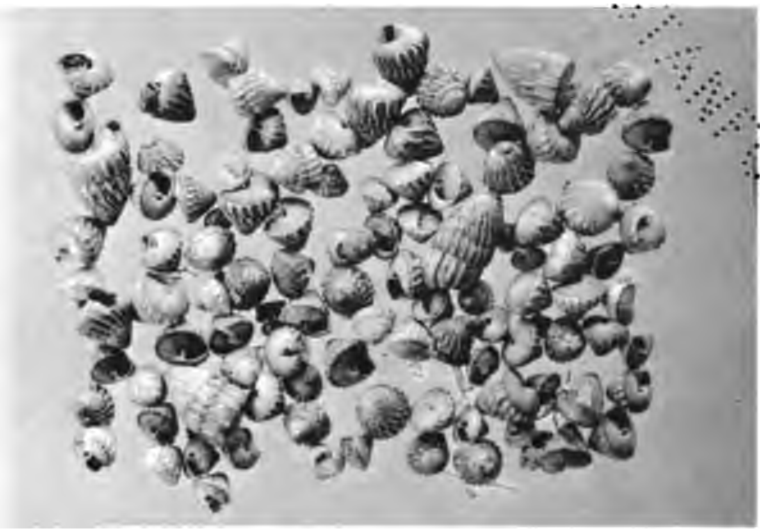
The three figures to the left are first generation of the "King's Road type" from the Second Ragged Key, north of Sands Key, Florida.

The four figures to the right are first generation of the "King's Road type" from Boca Grande Key, Florida.

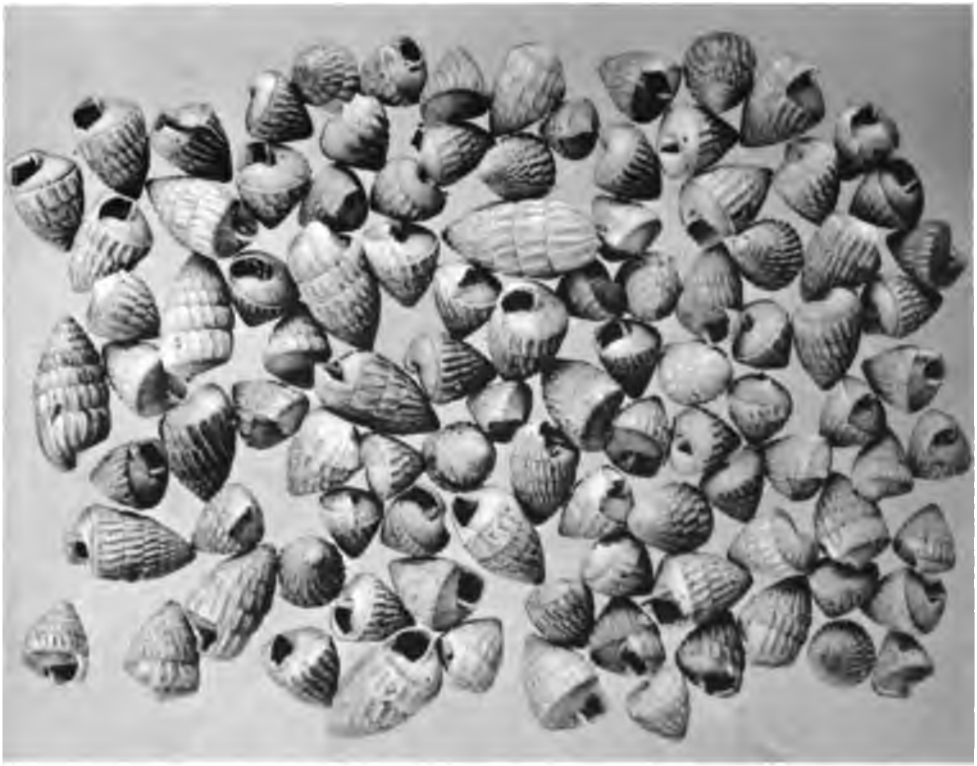
PLATE 4



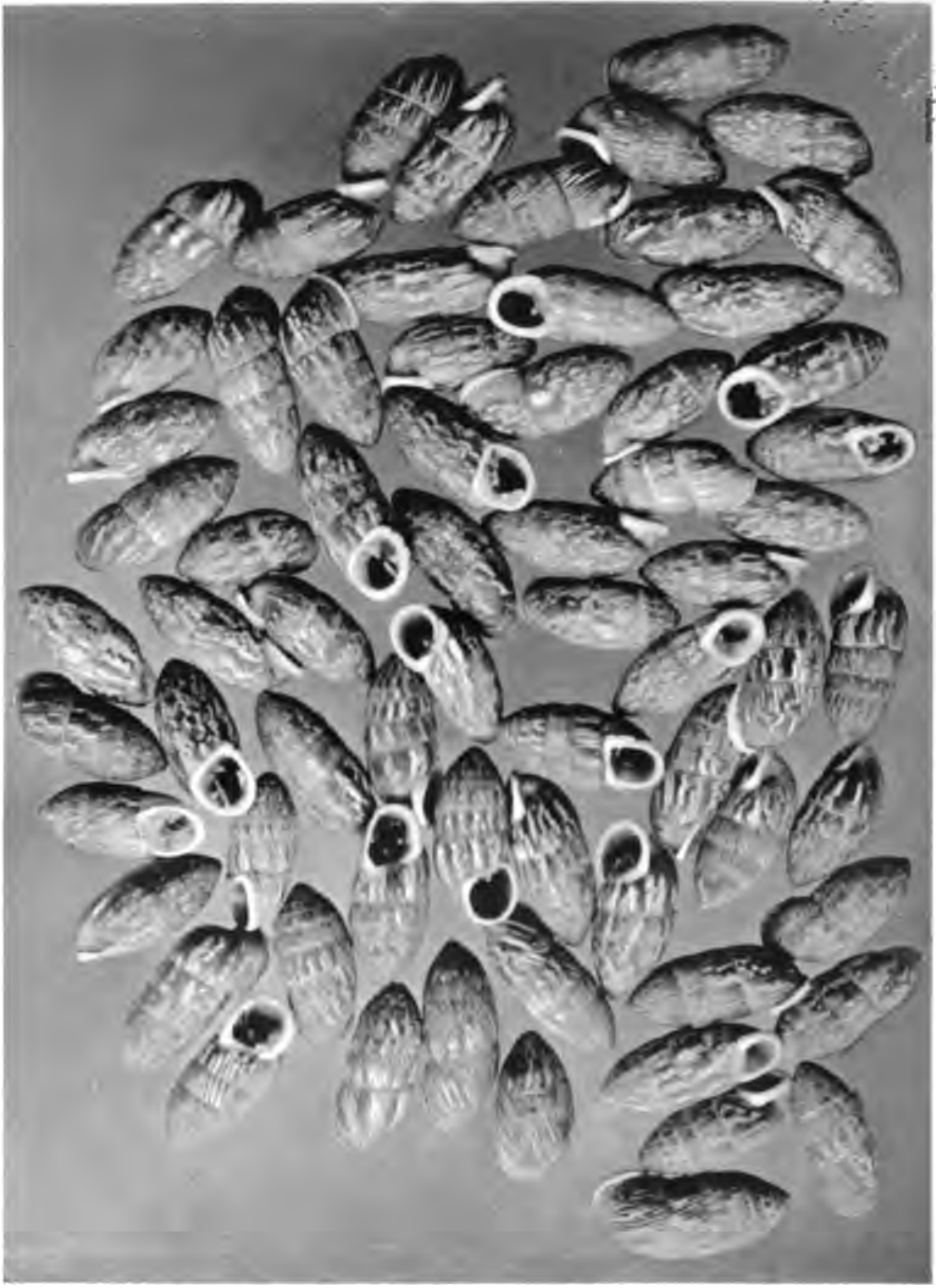
The young cerions of the "White House type," first generation from the North Colony of Loggerhead Key, Tortugas. These represent the new colony referred to as "Cerions—Y."



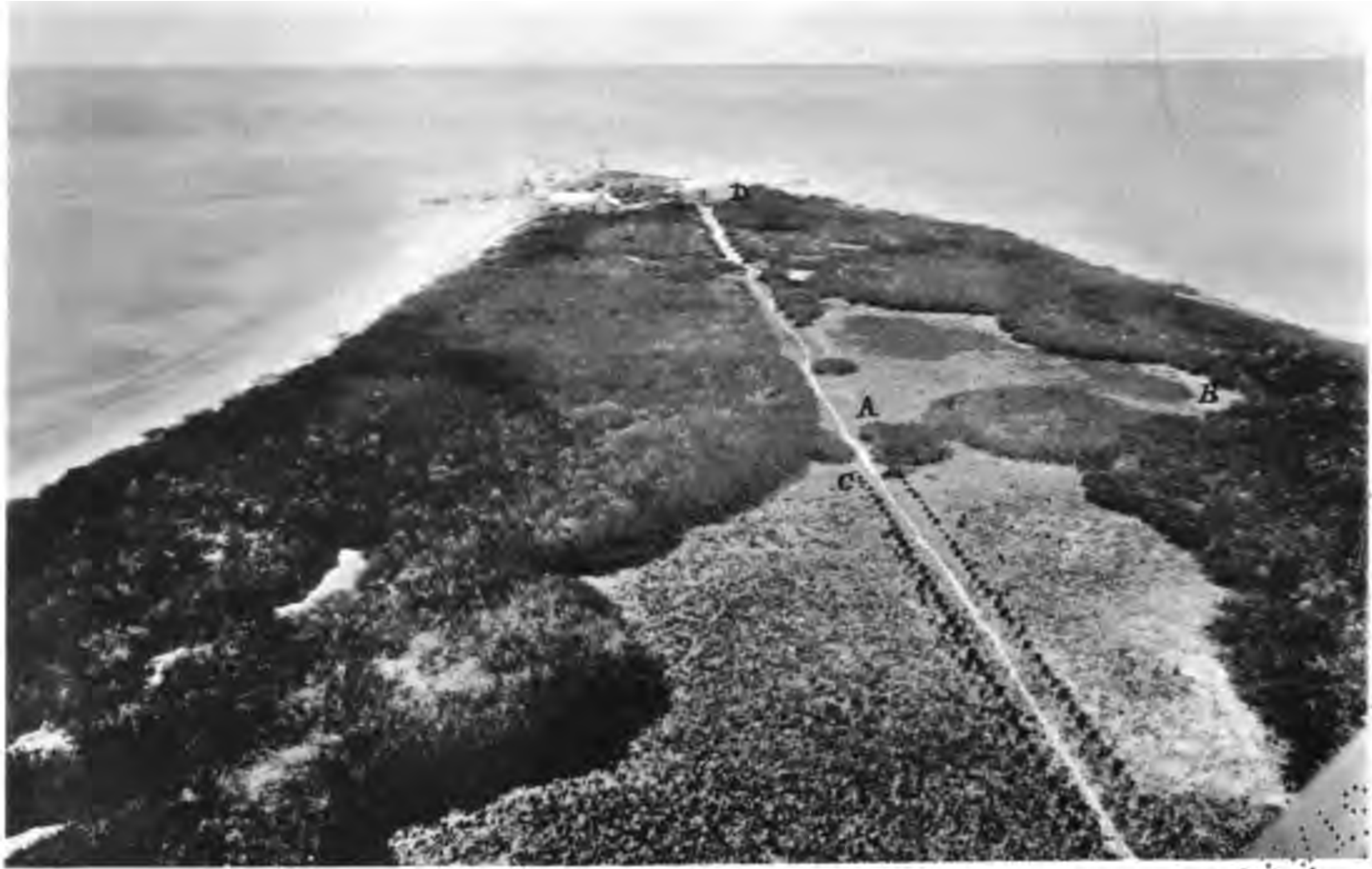
Young specimens of the "Kings Road type," first generation from the South Colony of Loggerhead Key, Tortugas. These represent part of the new colony referred to as "Cerions—Z."



The young cerions of the "White House type," first generation from the North Colony of Loggerhead Key, Tortugas. These represent the new colony referred to as "Cerions—Y."



"Mottled Cerions" representing the new colony bearing the label "Spring Hill, Nassau, 1914."
(Photographed by Dr. Mayer)



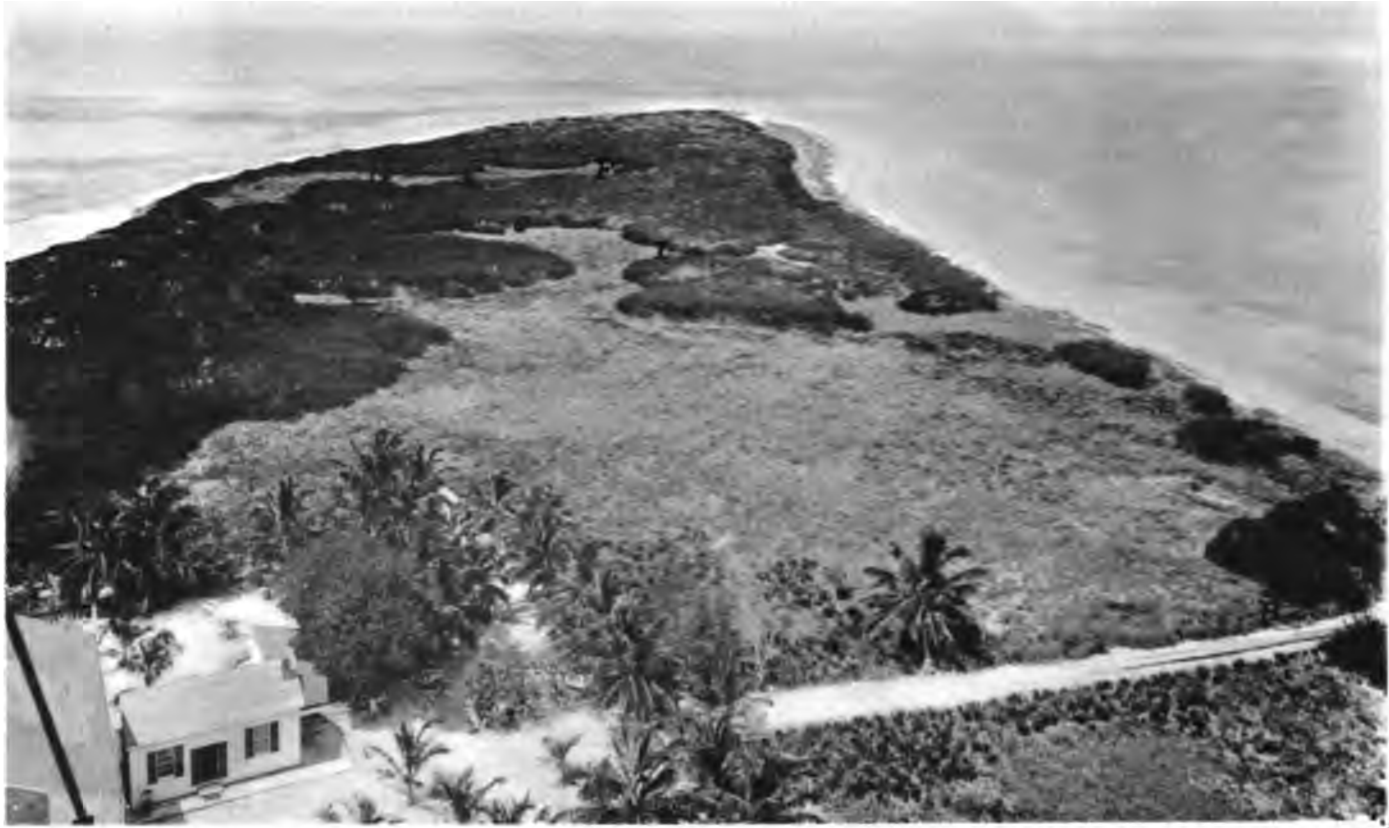
North End of Loggerhead Key from the Light House Showing Location of Cerion Colonies.

A—"White House type," 1912 planting.

B—"White House type," 1914 planting; (tag mark—"Cerions—X"). First generation from North Colony.

C—"White House type," 1914 planting; (tag mark—"Cerions—Y"). First generation from North Colony.

D—Mottled Cerions from Spring Hill, Nassau, New Providence, 1914 planting; (tag mark—"Spring Hill, Nassau, 1914").



SOUTH END OF LOGGERHEAD KEY FROM THE LIGHT HOUSE SHOWING LOCATION OF CERION COLONIES.

E—"Kings Road type," 1912 planting.

F—"Kings Road type," 1914 planting; (tag mark—"Bastian Point, Andros, 1914"). New importation.

G—"Kings Road type," 1914 planting; (tag mark—"Cerions —Z"). First generation from South Colony.

H—"Kings Road" and "White House types," mixed, 1912 planting.

I— Place to which the remnants of the above colony were transferred; (tag mark—"Cerions—XX").

IX.

STRUCTURE AND POLARITY OF THE ELECTRIC MOTOR NERVE-CELL IN TORPEDOES.

By ULRIC DAHLGREN,
Professor of Biology, Princeton University.

Six plates, six text-figures.

STRUCTURE AND POLARITY OF THE ELECTRIC MOTOR NERVE-CELL IN TORPEDOES.

Some time ago the writer noticed that the electric motor nerve-cell of *Tetronarce occidentalis*, a large torpedo found on the coast of Massachusetts in America, contained two nucleoli in its nucleus; and further, that these nucleoli were different from one another in form and in chemical composition, as shown by their staining properties and their optical properties under the microscope. The point of greatest interest, however, was the position of these two nucleoli, one always being dorsal and the other ventral in position in the nucleus. So invariable was this condition that it was decided to undertake studies of these cells, and for that purpose a visit was made to the Naples Station, where *Torpedo marmorata* and *Torpedo ocellata* are to be had. Here it was surprising to find that the electric motor nerve-cells of these two forms did not contain both the nucleoli found in *Tetronarce occidentalis*, but only one of them, the larger of the two, which always appears in the ventral position in the American form. This larger nucleolus corresponds to the body known to cytologists as the *plasmosome* and will be spoken of by this name. It is so evidently the same and shows such an evident tendency toward an orientation of its position that it was decided to prepare this paper chiefly with regard to the structure and position of the plasmosome in the electric motor nerve-cells of *Torpedo ocellata* and *Torpedo marmorata*, reserving the material already gathered upon *Tetronarce occidentalis* for a second part of this paper when further experiments can be made upon that eastern American fish.

This work will, therefore, consist of a description of the structure of the electric motor nerve-cell as found in *T. marmorata* and *T. ocellata* and an account and discussion of the literature and of the experiments which were performed by the writer in an effort to decide what physiological and chemical or physical factors were capable of influencing the position of its nucleolus or plasmosome. Incidentally, some more or less interesting results of the experiments which pertain only indirectly to the main point will be mentioned, as well as a few new facts concerning the structure of the cytoplasm.

I wish, at this point, to express my thanks to the Carnegie Institution of Washington for allowing me to occupy one of their tables at the Zoological Station at Naples in 1912–13. Also to the officers of that Station for many kindnesses and for the very efficient help given me in the course of my work.

As is well known, the electric organ of these fishes consists of two large masses of modified muscle, lying symmetrically on each side of the median line, as can be seen from the well-known figure of Fritsch (fig. 24, pl. 6). It should be noted that the brain lies midway between the two portions of the electric tissue in which the electromotive force is generated, and in a transverse section taken across the body of the animal as seen in figure 25, plate 6, we get a better view of this relation of the brain to the electric organ.

The two poles of the organ, which is possibly some form of multiple concentration cell, are + or anode on the upper or dorsal surface of the animal and − or kathode on the lower or ventral surface. First Cavendish and later DuBois-Reymond worked out the course of the current caused by this organ in the surrounding salt water at the time of discharge, and the diagram by Cavendish, as well as the later and more correct diagram of DuBois-Reymond, are shown in text-figures 1 and 2, respectively, where the field and its currents at the time of discharge are plotted. It can here be seen that the brain is theoretically lying in a current of some force running from the anode above to the kathode below, outside of the electric organ. These theoretical considerations have been proved to be true practically, by experiments in the laboratory conducted by the same great investigator, and it can thus be stated that the electric motor nerve-cells, in the so-called electric lobes of the brain, lie in a current that passes from above downward, or in the opposite direction from the current that passes through the tissues of the electric organs themselves.

A word as to the anatomy and general histological arrangement of the electric motor lobes of the torpedoes will be useful before proceeding. The muscle region which develops into the electric organ of this fish is innervated by fibers that proceed from the anterior or motor areas of the medulla oblongata. Owing, however, to their immense increase in size and the way in which they become massed in two symmetrical oval lobes, the two masses are forced by their growth up through the median wall of the medulla and come to lie in what appears to be a dorsal and sensory position (plate 6, fig. 26).

All the large cells in this mass, as will be presently described in more detail, have several processes, one of which is the neuraxon or efferent process. This neuraxon leaves the cell and, joining with other neurites from adjacent cells, all pass in these groups toward other similar groups, finally uniting to form the very large nerve-trunks that pass out of the ventro-lateral edge of the nerve-tract to go to the electric organs. Since the neuraxes pass downward on their course they usually leave or emerge from the ventral surface of the cell, but this is not true in all cases.

It is easy to see from this description and from plate 6, figure 26, and text-figure 6 that the functional polarity or axis of the cell is in a majority of cases dorso-ventral, or, as the fish usually lies, is up and down. But while this is true, a not insignificant number of cells are so placed that, in order to reach the larger general groups of nerve-fibers, their neuraxes must leave them from any of their lateral surfaces or even from their dorsal or upper surface (text-fig. 5).

Each of the cells in question is a typical nerve-cell of extraordinary size. They grow with the growth of the fish to a certain degree and in a well-developed fish, of say 35 cm. in length, these cells will average 75 microns in diameter. They are compact in shape, as the various figures will show, and each gives off from 20 to 40 processes, one of which is the neuraxon or main impulse-carrier from the cell to the electroplax which it supplies. The remainder are dendritic in structure and are thin and richly branching. Some traces of a weak polarity in the arrangement of the processes can be seen (plate 3, all figs.) in the fact that in many of the cells the neuraxon is given off at one end of a slightly elongated cell, while a majority of the dendrites are given off at the other end. In other cases this is not so apparent and the distribution of the dendrites seems to be very general and not restricted to any one area. Preparations made by teasing bits of electric lobe that have been macerated for 24 to 36 hours in one-third alcohol serve to show these features to advantage in plate 3, and in such isolated cells the processes can be seen for some distance, being seldom broken off less than the diameter of the cell in length, while in many cases they are shown for a much greater distance. There is seldom any difficulty in distinguishing the axis-cylinder process from the dendrites. It takes its origin from the efferent pole or end of the cell, which forms a large and fairly well-defined implantation cone and which is further marked by being at a somewhat thinner and tapering end of the cell and by being bounded by the larger mass of pigment material. The process is not noticeably thicker than the dendrites, but it holds its thickness for a long distance from the cell. Also, like the implantation

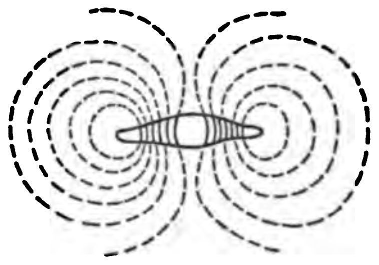


FIG. 1.

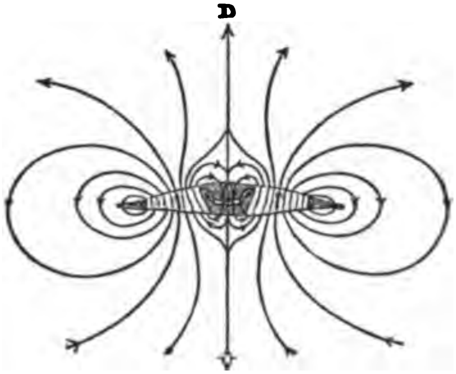


FIG. 2.

FIG. 1.—Diagram, after Cavendish, to indicate course taken through the surrounding water by the electric current generated at time of discharge of electric organ in *Torpedo marmorata*. Copied from "The Physiology of Nerve, Muscle and Electric Organ" by Dubois-Reymond, translated by J. Burdon-Sanderson. Oxford, 1887.

FIG. 2.—Improved and corrected diagram of same conditions as in fig. 1, by Dubois-Reymond. Copied from same source as fig. 1.

cone itself, it is clearer and more decidedly fibrillar in texture than the dendrites, being free from the chromophyllic substance which is found in these processes. In some cases the neuraxon is shown unbroken in the teased preparations for a distance of six or seven times the diameter of the cell. Plate 3 shows nine of these cells, in which the condition just stated can be easily seen.

The structure of the cytoplasm is of interest in regard to some possibilities as to a polarity and orientation of the elements of the cells. As observed in sections stained in most of the usual ways and in macerations of several kinds, and particularly by careful study of the living cells under the best and highest-powered lenses, it consists of the following substances:

First, a delicate protoplasm which pervades all parts of the cytoplasm as a reticulum. It is not stainable with the chromatic dyes and is only seen in certain torn parts of stained sections when deeply stained with eosin or acid-fuchsin. It is not easily distinguishable from the fibrillar substance which appears to make up the bulk of the cell-body. This fibrillar material is seen in both stained and unstained specimens as a "fibrillar mass" which passes into or out of the cell through both dendrites and axis-cylinder process and which forms at various points more marked paths through the cell-body than at others. It does not stain with the ordinary dyes and has been demonstrated by Apathy, Mann, Hatai, and others, to be, or to contain, a series of fine, sharp, and continuous fibrils running in bundles and courses that appear to be the possible pathways of the nerve impulse. As this material seems to determine no polarity of the cell that bears upon our main point, I shall not consider it further.

Another material is the well-known Nissl substance or chromophyllic substance, which appears in the form of fine granules. Its most prominent pecularities are that it stains with the chromatin dyes in a fairly strong way, that it has about the same index of refraction as the fibrillar mass in the living cell, and that, in this electric cell at least, its component granules are not sharply defined bodies, but seem to be soft or jelly-like in varying degrees, according to the fixation and staining processes that the cell is subjected to. It is scarcely visible in life (plate 2, fig. 3).

The arrangement of the granules in masses of various sizes, known as the Nissl bodies or tigroid bodies, is a natural one. They are packed by the various crossing and turning bundles of fibrillar substance into the spaces that lie between their various courses. Thus, they are often spindle-shaped or three-cornered. Also, where very many bundles of fibrils must be crowded into a compact parallel mass, these bodies are excluded as a mechanical necessity, as is seen particularly at the point in the cell where the axis-cylinder process is about to leave the cell, the implantation cone. The chromophyllic substance is also found to be lacking in the extreme periphery of this and other nerve-cells, where its absence has been accounted for in various ways by Rhode (30) and other writers. As this substance is also of no significance in regard to any polarity or orientation of the cell, it will not be dealt with further in regard to its properties or meaning and its literature will not be cited. It may be seen in a well-stained condition in figure 1, plate 1.

Another content of the cell was of more importance as a guide to polarity. This consisted of a number of granules of a substance first described by M. Shultze and subsequently more definitely by Garten (17 B). These granules were best studied by the writer in the living cell and then in macerated and teased specimens and lastly in sections. Their most prominent feature is only shown when studied in the living cell. Here they show a very high index of refraction, which disappears when treated with the usual clearing reagents. Thus these granules do not appear in unstained sections on account of their refractive properties. As Garten says: "am ungefärbten Preparat waren die Körnchen nicht sichtbar."

In fresh or recently fixed formalin material these granules were visible not only by reason of their refraction quality but also because of their color. This was much more noticeable in some cases than in others and in one case their color was a rich, golden-orange, like some of the lighter brown pigments found in vertebrate skin and elsewhere. The depth of color in the granules was found to correspond to the external and internal color of the electric lobes of the brain in which they are found and in *Torpedo ocellata* and *Torpedo marmorata* this varied from a faint yellowish tinge in fully 50 per cent of the specimens to the rich orange found in one or two examples as mentioned above. It thus would seem that in certain specimens this substance gives the lobes their peculiar color, but that whether colored or not the same granules exist in all specimens. The electric lobes of the large American torpedo, *Tetronarce occidentalis*, are but little different from the rest of the brain in color and it will probably be found that in this form the refractive granules are present but colorless. In *Narcine braziliensis*, the little torpedo of South America and the West Indies, the electric lobes are a very deep and brilliant orange in color, caused undoubtedly by the coloration of these same granular structures in all specimens.

In size these granules were variable and usually less than a micromillimeter in diameter. Some might have attained to this size. Garten speaks of them as round, but in the fresh cells many of them seemed irregular in shape and decidedly angular and elongate. In fixed and stained sections (plate 1, fig. 1) they appear round.

The fixation and staining of these granules seems difficult, and best results were attained by a quick, hard fixation with pure sublimate or Bouin's fluid and a rapid embedding. Figure 1 of plate 1 shows a case where Bouin's fixative containing 5 per cent potassium bichromate followed by a hard stain in iron hematoxylin has brought them out black. In every case where the decolorization was carried far enough to show the chromatin nucleoli the bodies in question were decolorized and could not be made out by the best lenses and refraction conditions. The alcohols took out any brown or yellow color that they possessed. I shall follow Held and Garten in calling them neurosomes.

These neurosomes were found scattered all through the cell-body (cytoplasm) and appeared to lie in much more intimate relation to the fibrillar substance than the Nissl bodies did. Thus they appeared to lie in spaces between the Nissl bodies. While scattered sparingly through the whole cytoplasm, they were gathered in large masses at the pole of the cell from which the axis-cylinder took its origin. Here they formed a thick ring around the axis-cylinder process and are to be seen in figures 10 to 18, plate 3, where 9 cells from two torpedoes are shown after bits of the electric lobes had been macerated and teased out on the slide. In this case the neurosomes were a rich golden brown.

In figure 3, plate 2, a cell is shown as it appeared in the living state under closed substage diaphragm, thus showing the parts of the cytoplasm by diffraction. The neurosomes can be very easily seen under this condition apart from any color that they may or may not possess. The neurosomes are also shown by the strongest osmic-acid fixations, but are not a fat of the ordinary kind (see Dogiel, 12 B). They are found in other nerve-cells and can be best seen in living tissue, pressed between the thin cover and a slide and examined with the highest powers and with the small diaphragm.

These "neurosomes" are the bodies that have often been described by all writers on the structures of the nerve-cell as "pigment granules," or collectively as the "pigment body." They have, perhaps, been best studied in the spinal ganglion nerve-cells of vertebrates, especially the mammals. Dogiel, in a review of the structures of these cells, in a book of comparatively recent date (12 B), describes them and cites a valuable list of writers on the subject who have discussed the structures from a physiological and chemical side. This summary, while not giving the substance a definite name, or associating it with any known function of the cell, does show the structures to be one and the same with the structures described above by the present writer and, further, clearly shows them to be a constant and specific organ of practically all nerve-cells rather than the products of senile or pathological nerve-cells. That they are closely associated with the functional polarity of the cell, as a nerve-cell, is clear from their concentration near the origin of the efferent process, but that they are not in any way concerned with the polarity of the nucleus under discussion is equally clear, and they will not be further discussed in this connection.

A slightly different and thin layer of homogeneous cytoplasm, the perinuclear cytoplasm, is found around the nucleus. It is marked off from the main body by a layer of fine granular material that appears in figure 3, plate 2. This layer becomes visible only in a few favorable fixations and stains.

The black-staining, thread-like bodies described by Solger (33) and the centrosomes, as well as the intercellular canals described by other authors in this torpedo, were not seen in the thirty or more fish whose brains were very carefully examined under all kinds of preparation, as well as in the fresh condition. Nor have the cells been studied yet for mitochondria.

NUCLEUS.

The nucleus of the electric motor nerve-cell of this fish is about 35 microns in diameter on the average, and attains nearly its maximum size while the fish is still small. Thus it increases but little in size from the 10 cm. size of fish to the 42 cm. size. It is placed at the approximate center of the cell and is but rarely far from this center, although in a very few exceptional cases it may appear at one side or in one end. In some very few cases two nuclei appear to occupy an extra-large cell. This appears to me to be rather a case of the cytoplasmic union of two cells in early life. The nucleus is inclosed in a smooth, even membrane of appreciable thickness and considerable staining power in the basic as well as in other dyes. This membrane, as the experimental work will show, is of equal thickness and apparently of equal chemical composition at all points and offers little of interest with regard to our question of polarity.

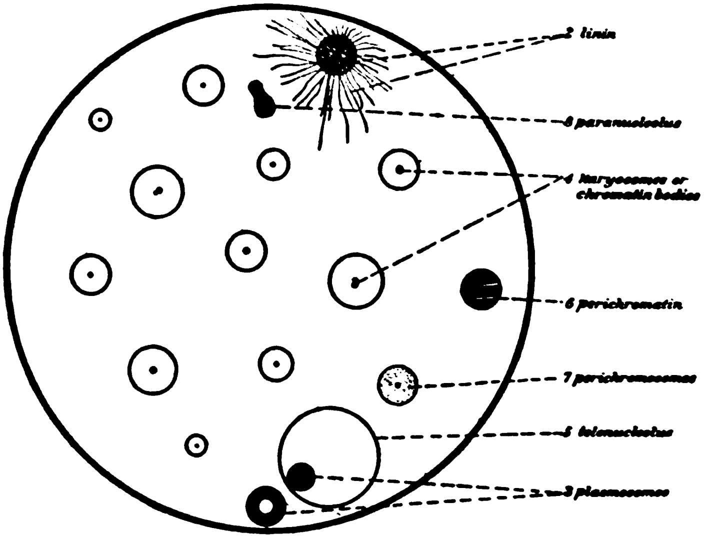


Fig. 3.—Diagram of nuclear content in electric motor nerve-cell of *Torpedo* and *Tetronarce.*

The contents of this membrane form a more highly differentiated mass than the contents of most other nerve-cell nuclei. This differentiation of the nuclear mass into at least six or perhaps seven distinguishable nuclear organs, as well as the large size of the nucleus, makes it an exceptionally favorable subject for study. While some of these structures are easily recognized as the same organs found in other nerve-cells, others can not as yet be so homologized and consequently their names may have to be changed when their real function becomes known by further study. The accompanying pen outline (text-figure 3) will serve to indicate the structures, with the names more or less temporarily applied to them. A more accurate drawing of the nucleus of this cell appears in figure 2, plate 1, as well as in figures 4 to 9, plate 2.

The contents of this nuclear membrane are at least six in number and will be considered in the normal cell in the following order: (1) *nuclear fluid;* (2) *nuclear achromatin* or. linin; (3) *plasmosome* or chief nucleolus; (4) *chromatin bodies* or *karyosomes;* (5) a more or less frequent and unknown body of nucleolar appearance which I shall call temporarily the *telonucleolus;* (6) the *chromatin* or *perichromatin* of Magini, a body which appears to be very closely connected with the chromatin nucleoli and contains a larger number of smaller bodies; (7) the *perichromosomes*, which are scattered through it in a regular order. The paranucleolus found in the nucleus of this cell in *Tetronarce* will not be described here, as it is not present in *Torpedo.*

The nuclear fluid can be dismissed with but short discussion. It is a questionable factor as an independent unit in the nuclear structure of this cell, and such of it as is not combined with the other elements of the nucleus must be looked upon as a non-vital element. This nucleus was put under the cell-dissecting arrangement of Barber and torn to bits with the glass needles. Under this treatment it was found that the nuclear membrane could be punctured or torn or even removed altogether and that the mass of the nucleus remaining was of jelly-like rather than of fluid consistency. This seems to show the absence of any large quantity of free liquid material during life. On the other hand, some of the best Flemming fixations, when the largest amount of nuclear material was fixed and retained, still showed some fine empty spaces, while in all other fixations much larger empty spaces are present in the nuclei, and these spaces must represent either shrinkage or fluids which have dissolved out. The evidence seems to show that both are true; that some little free and uncombined fluid is present in the nucleus and that this occupies very small spaces that are more or less enlarged by shrinkage of the remaining structures in the process of fixation.

The viscous, weak-staining, *non-chromatic* substance or *linin* of the nucleus will next be considered. This is probably a nucleo-albumen and is of a jelly-like consistency in the live cell. As may be seen in figure 3, plate 2, it is scarcely visible during life, although dark-stage oblique illumination would probably show it more plainly. In the living cell it can in no way be considered as the network or thread-like structure that we find supporting the nucleolar bodies after fixation. I think this is easily proved by the following facts: In torpedoes Nos. 20 and 4 the peripheral cells in control specimens show a centrally placed or ventrally oriented plasmosome and the accessory nucleoli distributed throughout the cell. It is evident, upon inspection of the drawing and preparations, that in that condition, and given the presence of such a fine-meshed network, the plasmosome and accessory nucleoli could not be moved without breaking all the meshes and threads through which they had to pass. And yet in figure 23, plate 5, from gravity experiment on torpedo No. 4, all these bodies are shown down on one part of the nuclear membrane, while the entire remainder of the nucleus is occupied by the well-fixed, fine-meshed alveolar reticulum. It must be true that the reticulation of the achromatic material is a result of fixation and that, while living, the nucleolar bodies can move or be moved through it without injuring its structure. On the other hand, too, in cells subjected to a stronger current of electricity (over 0.25 ampere) the various substances that are moved to the anode leave a thread-like reticulum that may be fairly considered to be a part, probably in some slightly changed condition, of the original structure of the nucleus.

Of course it would be possible to have a reticulum, or better an alveolum, through which the plasmosome might move as a wet marble could move through soapsuds or foam. But in this case the alveolar structure would undoubtedly show in life, which is not the case in this nerve-cell. Such a condition has been suggested by Murlin (27).

Further, it would be hard to determine how far and to what degree this material enters mechanically into the other structures of the nucleus. There is reason to believe that it is denser and firmer where it holds together the cloud of perichromatin around the chromatin particles, for under several circumstances this gathering of material moves as a unit and independently of the other similar clouds and other structures of the nucleus. Here it appears to have a radial arrangement.

The differences in the reticulum as found in different parts of the same preparation are in themselves of great interest. In figures 22 and 23, plate 5, are drawn two cells, one from a Bouin fixation and the other from a Flemming fixation, showing how the appearance of this achromatic substance differs according to the distance the fixative has had to penetrate in order to reach it. This difference also comes out in figures from different preparations, and where one has studied many preparations he can at once say about how far from the surface the fixative had to penetrate to get to each cell.

A proper fixation of the nucleus of these nerve-cells is a fairly difficult matter and many papers on the subject (otherwise excellent) show figures that indicate much deficiency in this respect. And this is aside from those cases where the whole nuclear content has been piled up in a broken mass. Some of the best workers on the structures of the cytoplasm have left us figures that give no true conception of the structures of the nucleus. Much careful work remains to be done upon it before we possess an adequate picture of its organization.

The plasmosome is one of the most prominent contents of the nucleus. It is large, being usually about 7 microns in diameter when single, and is an almost perfect sphere. Its most prominent physical property is a dense refractiveness which makes it easily visible in the living cell even under a wide opening of the condenser diaphragm. As the diaphragm opens, the outline of the plasmosome lasts a trifle longer than that of the nuclear membrane, and when one considers the greater radius of the nuclear membrane this means that the plasmosome is the most refractive body in the cell, excepting perhaps the karyosomes. No accurate measures have been taken to measure the actual refrangibility of the various organs of this cell by accurate physical means, but it is hoped that this will be done at another time.

In perhaps a majority of cases the plasmosome is a single body, but this factor varies in the different individual fishes examined. I think it may be safely stated that in the oldest and largest specimens the plasmosome is most apt to be single, while in younger specimens it is most apt to be a multiple body. Also a distinct tendency to vary in the distribution of the plasmosome was observed in individuals of the same size and sex. When multiple, it is most usually found as a single large body with one or more smaller masses in some other (usually distant) part of the nucleus. Or in some cases it may be found as two fairly large spheres of approximately equal bulk. In one *Torpedo ocellata* of 15 cm. each nucleus appeared to contain its plasmosome as four or more bodies of equal size, any one of which was much smaller than the usual size of 7 microns. In all cases of multiple plasmosome it appeared that the total volume of the various bodies was greater than that estimated in the nuclei where a single body appeared. It may be said here that in the large American *Tetronarce occidentalis* a single plasmosome is almost the invariable rule.

The plasmosome is by no means a homogeneous body. In the large and typical forms at least three substances may be distinctly seen in it. One is a granular, non-refractive, and non-staining content of the various "vacuoles" found in this structure. The principal vacuole occupies a large part of the exact center or, in numerous cases, a more or less eccentric position in the body of the plasmosome. The usual diameter of this vacuole is a little more than half of that of the whole plasmosome, or 4 microns. It is always round and "bubble-like" and in some very few cases is so close to the periphery of the plasmosome that it has broken through and is open to the other contents of the nucleus. The edges of the plasmosome thus broken are rounded up as though by surface tension, a condition that probably exists between the vacuole and its surrounding shell of the denser plasmosome material.

This remaining or peripheral portion of the plasmosome is, as has been indicated, the dense and refrangent portion of the structure. It usually contains in its substance a large number of much smaller "vacuoles" of about 1 micron in diameter. These are, to all appearance, exactly like the one larger vacuole, except in size, and in one other respect to be mentioned in the next paragraph.

This thick, refrangent shell of the plasmosome is apparently made of two very similar layers that slightly differ from each other in staining capacity in the various stains used. The inner layer is darker-staining and also thinner. It surrounds the large chief vacuole, but does not extend around from the outer layer; is not sharp, but distinct, and no surface tension appears to exist between the two substances.

In the smaller plasmosome the vacuoles are not so completely developed and they are all of one size in the smaller bodies, or in the smallest may even be absent or a single vacuole may exist.

The staining power of this outer part of the plasmosome appears to be a function of its physical rather than its chemical properties. Thus in the regressive stains, as iron hematoxylin, it first appears very black, but when the decolorization is carried past a moderate point the color suddenly comes out, leaving only a light-gray shade, while other chromatic bodies of much smaller size have retained the black color. The stain does not always come out evenly, but often in patches. If the sections are thick the decolorization of the plasmosome may be long deferred, owing to the slowness of diffusion through its thick and dense body rather than to its chemical relation to the stain.

In connection with the plasmosome another substance exists which is not so easily seen in many preparations, but which came out clearly and undoubtedly in material from *Torpedo ocellata* that had been fixed in pure sublimate and stained with safranin. This is the thin layer of chromatic material first discovered in other cells and published by M. Haidenhain in 1892. It forms a very thin and somewhat roughened covering of the entire exterior of the plasmosome and can very easily be overlooked in many specimens because it is either obscured by the total staining of the plasmosome, or if the plasmosome is decolorized enough to be clear, this chromatic shell is also decolorized. If looked for with care and in such a preparation as the above it comes out with entire clearness.

The morphological position of the plasmosome is the principal object of study in this work and will be considered after this general description of the nucleus and before and together with the experimental work.

The peculiar body which I have only recently found in the nucleus of *Torpedo ocellata*, and which I shall call temporarily the telonucleolus, is next to be described. This structure is only to be found in a comparatively small proportion of the nerve-cells in a given electric lobe, and this proportion appeared to vary in a number of counts that were made from as much as 35 per cent to as low as practically nothing. It seems that the smaller fish had the larger proportion and also that the presence of this body was in some way related to the fish that had the plasmosome distributed in several bodies, some of which were small.

This telonucleolus appears as a hollow sphere, often larger than the largest plasmosome and seldom smaller. Its wall is composed of a clear, sharply defined membrane that is less stainable than any other material in the nucleus, even refusing to become colored with such counterstains as eosin and erythrosin, or para-carmine and hemalum. It is also refrangent, and this property makes it easy to see at once when it is present in a cell. I have not measured its refrangency as compared with other structures in the cell.

The thickness of its wall is inconsiderable, but could be accurately measured. This wall was continuous and appeared to be more or less impermeable to most liquids, because the only cases in which the sphere appeared to collapse were when it was cut by the knife in sectioning. It appeared to collapse and crumple quite completely, showing that its walls were either very thin or that they had very little rigidity.

The content of this telonucleolus appeared to be a fluid, and a very slight and non-stainable reticulum of "linin." Besides these, in practically all cases it also contained a very small plasmosome which was in no way different from the other plasmosome bodies in the nucleus. This contained plasmosome was usually so small, however, that it had only one or two of the plasmosome vacuoles and the inner, darker-staining layer of the refractive shell did not appear to be developed. As the same is true, however, for plasmosomes of this small size that are found outside of the telonucleolus, it is safe to say that all the plasmosome bodies in the nucleus possess the same kind of structures, whether within or without the telonucleolus.

The position of the telonucleolus is peculiar and has some unknown significance. It is always found close to or touching one of the plasmosomes, large or small; further, the little plasmosome inside of it is also oriented in the telonucleolus against the side which touches the external plasmosome. This is well shown in figures 4, 6, 7, and 9 of plate 2.

I am inclined to believe that this telonucleolus plays some part in the development of the plasmosome content of the nucleus along with the multiple plasmosome found in the smaller torpedoes, but am not prepared to say what part, until I have completed some histogenetic work now partly done. The telonucleoli are not found in all of the cells and are sometimes hard to find.

Another content of the nucleus consists of a number of small spherical bodies which, on account of their high refrangency, sharp spherical outline, as well as their strong chemical affinity for basic dyes, I shall call the *karyosomes* or *chromatin nucleoli*. These bodies have been mentioned by Garten (17 B) and others, and have been more carefully and particularly described by Magini in connection with a new substance which he calls *perichromatin*, in a paper published by him at Montepulciano in 1901 (24 D). My results do not in any way conflict with the morphological facts brought out in this excellent paper, but I believe that in Magini's work and in mine the chemistry of several of the bodies described is not sufficiently understood to designate any one of the three of them as the same substance as the chromatin which goes into the chromosomes of embryonic tissue cells that are dividing by mitosis. This chromatin is surely to be found among these bodies and my separation of them will be a little more close than his was, but histogenetic, experimental physiologic, and chemical work will be necessary for a sufficient understanding of the subject. Only in failing to distinguish chemically (by color) between his "filimento nucleinico a gomitolo" or "rete cromatica" or "granuli cromatici" and his masses of perichromatin, do I find myself differing, and I still hope to find some true or basichromatin disposed in this way with other staining methods.

These chromatin nucleoli are rather larger and more abundant than Magini states in his paper. The largest one measured in my preparations was fully 2¼ microns in diameter and many could be found that measured 1¼ to 1½ microns. Many also are found below 1 micron in size, although these very small ones do not seem to grade down to an excessively small granule.

In the fresh state the chromatin nucleoli are visible and appear to possess a fairly high index of refraction, although not quite so high as that of the plasmosome. They are colorless and motionless and appear to be quite equally distributed through the nucleus. The larger ones are farther apart than the smaller. Some are placed directly against the nuclear wall and others at various points in the nuclear space. One of them is sometimes found against the side of the plasmosome.

In a considerable number of cases these bodies are grouped together; that is, instead of one being found at a single central point, two or more will appear, closely placed and apparently acting as a unit in the arrangement that has been mentioned. When so grouped, the supernumerary granules are usually very small, although sometimes two large ones will be found acting together.

These spherules or chromatin nucleoli are homogeneous and are about the most easily stained bodies in the nucleus. Their staining powers differentiate them at once from any other nuclear content. Particularly good to show the chemical difference in staining are some of the bulk stains, as a double staining with paracarmine and hemalum or borax-carmine and hemalum. In either of these two, with strong decolorization, the chromatin nucleoli take a deep, bright, transparent red or scarlet, while all plasmosomes will appear of a very light and delicate pink. This is in spite of the larger size of the plasmosome, which if it had an equal chemical affinity for the dye would stain much darker on account of its much greater diameter or thickness. The same is true of sections stained with safranin.

In the fresh specimen the structures that support these chromatin nuclei are almost invisible. With strong oblique lighting a slight suggestion of a supporting framework or reticulum of linin can be seen. In the fixed specimens, however, such a supporting reticulum appears and with most fixations it can be seen that the chromatin nucleoli are embedded in the larger masses of linin that lie at the centers of this reticulum. Further, it may be seen that the linin substance is arranged in a radiating fashion about the chromatin nucleolus in a way to form a sphere which is about the size of, or a little smaller than, the plasmosome and which has a fairly clear boundary or limit. This sphere, when it contains the "perichromatin" of Magini, together with the central granules which have been described as the *karyosomes* or *chromatin nucleoli*, represents the "spherule" of Magini, which he has so accurately described in his paper as the new substance of the electric motor nerve-cell. I have myself also observed and described in a histological text-book (Dahlgren and Kepner) (**11**) similar or probably identical structures in the large nerve-cells found in the motor ganglia of Cephalopoda.

I have been unable to prove any chemical or physical difference between the achromatic substance of these spheres and the remainder of the linin reticulum. The only differences observable are mechanical—the larger size of the sphere and its fairly regular radial arrangement. Its principal and only chemical (?) mark of distinction from the remaining linin is the fact that in some fixations it holds the substance called by Magini the "perichromatin," which he shows to have important staining qualities that differ from the other colorable materials in the cell. Its strong inclination to dissolve in certain media make it somewhat hard to show. Magini showed it best, according to his decriptions (unfortunately he had no figures), by fixation in osmic acid and staining in safranin. In my preparations it is best seen in iron hematoxylin stains after sublimate and formalin-alcohol fixations. Some of the best fixations, as Flemming and Bouin, show it entirely dissolved, or at least not visible in any manner whatever; other stains show it weakly visible, while some show it as a dense cloud gathered in a sphere about the karyosomes and staining a decidedly different tint from them.

Scattered in a spherical cloud in the mass of perichromatin are a number of small granules, much smaller than the central karyosome and also not strictly spherical in shape, as it is. These granules I shall denote as the *perichromosomes.* They may be angular in shape and the largest of them are far smaller than the smallest karyosomes. Like the karyosomes they take basic dyes and in the best sublimate fixations they also stain black with iron hematoxylin. These perichromosomes were not differentiated by Magini from the general mass of perichromatin of the spherule.

The perichromosomes are much smaller and more numerous than any of the karyosomes; it may be said that they form a group of granules grading down from the less numerous larger ones to finer and more numerous, until the successive sizes become so small that they can no longer be seen. Hence, it is possible that the visible perichromosomes are not different in substance from the mass of perichromatin in which they lie. They appear in most cases to stain in much the same way as the cloud of finer perichromatin in general, and this perichromatin usually stains differently from the karyosome in its midst. The larger perichromosomes are faintly visible in the fresh state. They seem quite a different substance than the karyosomes.

Taken as a mass, each karyosome, together with its spherical surrounding framework of linin in which are dissolved or borne as fine granules the perichromatin and perichromosomes, forms a unit which is, as has been said, of about the size of a full-sized single plasmosome. It will be convenient and perhaps permissible to call these complete units the "chromatin bodies." It is possible that they are the same as the chromosomes of dividing cells.

It may thus be seen that in the adult electric motor nerve-cells of the torpedoes in general there are at least six apparently separate materials which are not dissolved by the usual fixatives by subsequent handling with reagents, and which can be recognized and compared by their size, shape and staining capacity as well as, in some cases, by their specific gravity and their refractive index.

I regard these substances as organic compounds that take part in the life and activity of the nucleus and therefore of the cell, but some of which, at the time the cell is fixed in a more or less solid state, are possibly in a state of storage or temporary disuse. The reason for their solid form is a question of segregation of the particular material involved. This does not imply that the material in question is not active, for it probably is, but it does seem that it is necessary, for physiological-chemical purposes, that it be more or less concentrated at some particular point. Nor is its solidity an absolute one, but consists of varying degrees of gelatinization or even of strong solution, which are usually much intensified by the fixation, etc. Many other constituent substances of the nucleus must be in the form of solutions that are not precipitated by our fixatives and are consequently not ordinarily studied. Some of the latter substances are sometimes precipitated and preserved for study, and sometimes they remain in soluble form or are even converted from solid and gel forms to a solution by some fixatives. Thus many substances that are fixed and retained by osmic acid, formaldehyde, alcohol, and chromic acid are either dissolved or lost as an unchanged solution when the cell is fixed in pure sublimate, picric acid, or in Perenyi's fluid.

Thus when we find an important element, the "paranucleolus," present in *Tetronarce* that is not to be distinguished so far in *Torpedo,* and when we find another element the "telonucleolus" in *Torpedo* which has not been seen in *Tetronarce,* I believe that both of these elements must be present as a functional material in some form in both of these fishes. The cells are genetically closely related, they are used for the same identical purpose, and are both adult and in normal condition, and the apparently missing element in each case must be present in some form, possibly as a solution. For this reason the names applied in the present paper do not seem entirely satisfactory to the writer, in that they do not express the actual functions and chemical constitutions of the cell organs of the nucleus. Nor do all of these names permit of satisfactory comparisons being drawn between the nucleoli to which they are applied and to other nucleoli in other cells. It is certain that in this large nerve-cell we have a very high degree of differentiation of the nuclear organs and, apparently, an opportunity to make more exact studies of their identity and function than in any other cell, unless perhaps the egg-cell. And even in this respect the highly differentiated somatic cell such as that under consideration must be carefully studied and its elements traced back to the egg-cell before any general conclusions can be drawn about the meaning of the elements and their various activities in the nerve-cell.

LITERATURE.

The normal cell having been carefully studied, particularly as to its nucleus, the literature on the orientation of the nucleolus in *Torpedo* and experiments made on cells of *Torpedo marmorata* and *Torpedo ocellata* was next looked up to find any observations and experiments as to the question of a polarity of its nuclear contents. Such work had been done, mostly by Italian observers, and in particular by Professor Magini of Rome, who first observed a partial polarity of the entire nerve-cell in this fish (24). He examined many specimens of torpedoes at Naples and found that when the animal was killed by a violent death, as cutting by knife (vivisezione), the plasmosome was always found lying against that side of the nuclear wall which was nearest the *axone.* He believed at the time that the axone always left the cells in a ventral direction, and that this was therefore always an orientation in the direction of the axone when it was a ventral orientation.

He found further that the entire nucleus was moved slightly in this same direction through the cytoplasm of the cell and that in consequence a crescentic space was left on the side of the nucleus opposite to that to which the plasmosome moved. He interpreted this as a symptom of the electro-motor activity of the cell. Again, it should be noticed here that he figured all his cells as giving off their neuraxes in a ventral direction and all the plasmosomes therefore as moving toward or orientated toward the neuraxes. This we now know not to be a fact. Figure 4 represents Magini's conception of this orientation.

In adult examples which were allowed to die slowly out of water by asphyxiation, and which consequently did not give many or violent shocks from their electric organ, Magini found, on the other hand, that the plasmosome was usually central in position, and when eccentric its eccentricity was slight and in various directions. Neither did the crescent-shaped space appear on the dorsal side of the nucleus.

He also found that in very young specimens (7 cm.), whose electric organs were not yet well developed, the plasmosomes in the electric motor cells were always central.

He deduced from these three observations that the movement of the plasmosome ("nucleolo") from a central position in a state of rest to this eccentric position just after extensive and continuous activity was an accompaniment of the normal and extensive physiological activity of the cell at time of the discharge, and he further concludes that this movement of the plasmosome is the initial phenomenon which precedes and causes the nerve action of this cell. (Magini, p. 3.)

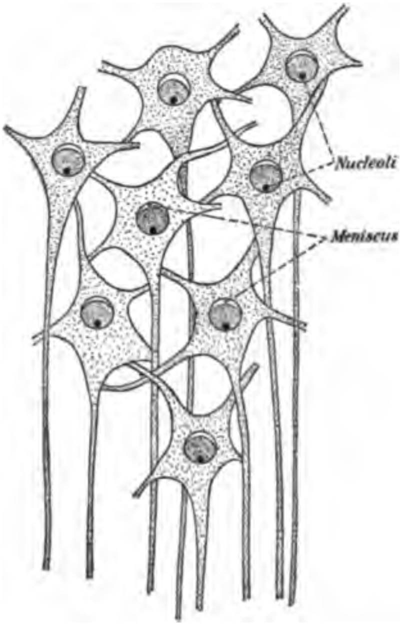


FIG. 4.—Sketch of a group of electric motor nerve-cells from *Torpedo*, as described by Magini in the adult after death by vivisection.

Coggi (8) took issue with these conclusions, being of the opinion that Magini's results were artificial and had been due to the osmotic action of some of his fixatives in the cases when the plasmosomes were found oriented in the ventral position, and especially in those cases where the entire nucleus had moved ventrally. The writer, being interested in the American form, *Tetronarce occidentalis*, in which an undoubted orientation of the plasmosome always exists, carefully studied 24 torpedoes at Naples in the winter of 1912–13 and investigated the following points: (1) Is there an orientation of the plasmosome? (2) Granted this orientation, is it due to the temporary physiological activities that initiate those processes in the cell which result in the nervous and the electric discharge? (3) Is it, instead of such a physiological phase, a permanent condition for a considerable period of the animal's life (adult life or later adult life)? (4) In case the third proposition is true, is this orientation of physiological value to the working of the cell (induction of electro-motor impulse) or is it of no significance to this activity? (5) In case it is not a condition that lends itself to the physiological activity of the cell, is the orientation due to the physical properties of the nuclear organs with reference to the electric current that passes through these cells at the time of discharge of the electric organs? (6) In the same case as just precedes, is it due solely to differences in the specific gravity of the various nuclear organs and particularly to the greater weight of the plasmosome?

The question of the orientation of the entire nucleus in the cell as described by Magini, *i. e.*, its apparent movement in a ventral position with the accompanying meniscoid space on its dorsal surface will be considered with the question of the polarization of the nuclear organs.

ACCOUNT OF THE EXPERIMENTS.

Torpedo ocellata, No. 1, 15 cm. long (small), killed with knife; gave many shocks before and during operation; plasmosome placed in various positions in nucleus, often touching some part of nuclear membrane. About 80 per cent show a tendency to be ventral in position. A few cells contain multiple plasmosomes. A larger number of telonucleoli than in most examples. Perhaps 10 per cent of the cells show it.

Torpedo ocellata, No. 2, 16 cm. long (small), killed with chloroform vapor. Plasmosomes single and sometimes double; one often lighter than the other in a varying degree. About 65 per cent decidedly ventral in position and resting against the nuclear membrane: Few telonucleoli. Some multiple plasmosome.

Torpedo ocellata, No. 3, 30 cm. long (large), pithed with knife, many shocks. One side of the electric lobe was subjected to a direct current of 110 volts in the usual glass tube with a diameter of 4 mm. and a length of the tissue mass of 1 cm. Direction of current was from anterior to posterior. Sublimate fixation. Current was weakened by some resistance.

The other side of the electric lobe was subjected to 543 times gravity in the centrifuge for 1 minute, then fixed in Bouin's fluid. Plasmosome was thrown from a normal position to the + side of the nucleus and against the nuclear wall. Force exerted in an anterior-posterior direction. A considerable amount of natural ventral orientation was indicated by the new position of the plasmosomes. Plasmosomes single in cells. No telonucleoli observed.

Torpedo marmorata, No. 4, 30 cm. long (large), killed with knife; many shocks before operation. Plasmosomes show very well-developed ventral orientation, about 70 per cent. Many cells seen where neurite goes off from either side or from dorsal side, while plasmosome is typically oriented on ventral side of nucleus and touching nuclear membrane. No telonucleoli observed. Plasmosomes single. A number of nerve processes traced from various positions of origin in different cells.

One bit of tissue was centrifuged for 30 minutes at 828.5 times gravity. Force was exerted from head toward tail or at right angles to any possible axis of orientation.

Another was subjected to 110 volts of direct electric current in usual tube of 4 mm. diameter; 1 cm. of tissue for 4 minutes. Tissue was "cooked" and then fixed in Bouin's fluid.

Torpedo marmorata, No. 5, 35 cm. long (large), killed by cutting and the brain divided tranversely through the electric lobes. The posterior portion was fixed at once in Flemming's fluid, while the anterior part was subjected to direct current of 110 volts. The tissue was inclosed in a 4 mm. glass tube and was 1 cm. long. The current was applied for 30 seconds and the tissue became "cooked" or whitened, with a discharge of gas at the kathode.

Torpedo ocellata, No. 6, 36 cm. long (large), killed by cutting out the brain-case. Electric lobes placed in glass tube 1 cm. long and 4 mm. square; area of lumen and direct current of 4 volts was run through for 1 hour. Tissue not "cooked." Was then fixed in Gilson's fluid. No control. Current passed through cells in anterior-posterior direction.

Torpedo ocellata, No. 7, 12 cm. long (small), worried so as to produce shocks and then killed and the entire brain removed by cutting with knife. Brain was then placed entire in 4 mm. tube. Anterior end cut off until length of mass was 1 cm., submitted to a current of 4 volts for 40 minutes, when current was 0.25 milleampere. Current was from posterior to anterior in direction. Plasmosomes scattered in a general distribution which was decidedly median in character. No control having been taken, it is assumed that the current did not modify the position of the plasmosome in any way.

Torpedo ocellata, No. 8, 11 cm. long (small). This fish was inclosed in a wire cage so as to force it to lie on its back. It lived thus, apparently comfortably, for 8 days, when it was removed and killed by the knife while upside down, and the brain (still upside down) was fixed, embedded, etc., all in the inverted position. The electric motor nerve-cells showed no orientation whatever. The fish had given many strong shocks before being killed.

Torpedo ocellata, No. 9, 16 cm. long (small), killed with knife after being worried, and electric lobes placed in centrifuge for 2 minutes at 40.60 times gravity. Force was applied from anterior towards posterior direction, then fixed in a mixture of one-half Bouin's fluid and one-half potassium bichromate 5 per cent. At this comparatively low centrifugal force the contents of the nucleus were not visibly disturbed. Notwithstanding the centrifuging it was still possible to count the percentage of ventrally placed plasmosomes. This amounted to about 15 per cent. A stronger force applied by the centrifuge, in this case, would have thrown the plasmosomes in a posterior direction inside the nucleus, but it would have still been possible to determine the percentage of ventral orientation, since the plasmosome does not come to rest at a dead center, but inside of a considerable arc, its position in which indicates its former amount of orientation in a line at right angles to the centrifugal force applied.

Torpedo marmorata, No. 10, 27 cm. long (medium), killed with knife; few shocks. Fresh tissue was examined and showed most of the plasmosomes in a median or nearly median position in the nucleus. A small portion of the posterior part of the electric lobe was cut off and fixed as a control. The remainder was placed in the glass tube of 4 mm. diameter and with the tissue extending over 1 cm. in the tube. This was then placed on a circuit of 110 volts with a lamp of 10 watts inserted as a loop which embraced a lamp of 16 watts and the amperage registered 7 milleamperes. It was subjected to this current for half an hour and the tissue fixed in Bouin. The current passed in an anterior-posterior direction.

Torpedo ocellata, No. 11, 42 cm. long (very large), killed with knife; numerous shocks. Living cells examined. Neurosomes particularly evident because of their dark golden-brown color. Plasmosomes found both in fresh cells and in sections to be oriented against the ventral side of nuclear membrane, at least 95 per cent.

Torpedo ocellata, No. 12, 30 cm. long (large), killed with knife; strong shocks. Neurosomes light yellow. In the prepared sections only about 25 per cent of the plasmosomes were oriented ventrally. Plasmosomes of usual size and but few cases of multiple plasmosomes.

Torpedo ocellata, No. 13, 35 cm. long (large), killed by cutting out brain; shocks. An evident cross between *ocellata* and *marmorata,* which often occurs. White spots with blue centers missing and the marbled markings of *marmorata.* No experiments. In the prepared sections the plasmosomes were 95 per cent oriented against the ventral wall of the nucleus. The plasmosomes in most cases did not quite touch the membrane. A single normal-sized plasmosome was present in practically all cases.

Torpedo ocellata, No. 14, 30 cm. long (large), killed with knife; many shocks, no experiments. In the preparations the plasmosome was single and only about 30 per cent were oriented ventrally. A rather smaller size of plasmosome appeared to be due to fixation or to the alcohols.

Torpedo ocellata, No. 15, 38 cm. long (large), killed with knife; many shocks. Plasmosomes show a decided and almost perfect ventral orientation. Very few exceptions. One or two plasmosomes displaced by knife, very easily diagnosed. Plasmosomes touch or nearly touch nuclear membrane. Variation of line of orientation from ventro-dorsal line amounts to less than 15°. Plasmosome almost always single.

Torpedo marmorata, No. 16, 42 cm. long (large), killed with knife; few shocks. Plasmosomes show a perfect ventral orientation against wall of nucleus. Variation of line of orientation from dorso-ventral line seldom more than 10°, except on dorsal edge, where a few exceptions occur. The remote cells with neurites leaving on other than the ventral edge were carefully examined and it was seen that the plasmosome does not move to the side of the nucleus next to the neurite.

Torpedo ocellata, No. 17, 32 cm. long (large). This fish was killed by placing in a large dish and inverting a box over this, so that the vapor from a sponge saturated with chloroform would pass into the water and thus into the fish's circulation. Later the box was removed and water that had been saturated with chloroform vapor was added until the fish was dead. When muscular action had stopped, and just before death, the fish began to give a succession of single shocks spaced in such a way as to lead one to think that each was synchronous with a single heart-beat. In the preparations 85 per cent of the plasmosomes were oriented ventrally. A single plasmosome was the rule.

Torpedo ocellata, No. 18, 30 cm. long (medium), killed with the knife; worried before killing, so that many shocks were given off. Electric lobe fixed in Bouin's and Flemming's fluid. 90 per cent of the plasmosomes were found to be ventrally oriented. Plasmosome single.

Torpedo ocellata, No. 19, 34 cm. long (large); allowed to die in an undisturbed condition in air; back uppermost, no shocks perceived. Died in about 10 hours. Orientation of plasmosome not definite, but estimated at something over 10 per cent.

Torpedo ocellata, No. 20, 37 cm. long (large), killed with knife; brain centrifuged in skull for 30 minutes, at 2,000 revolutions per minute, 14 cm. radius. Force applied from ventral toward dorsal surface. Fixed in Bouin, pure sublimate-acetic, and Flemming's fluid.

Torpedo ocellata, No. 21, 35 cm. long (large), killed with knife; shocks. Brain in 96 per cent alcohol. All cells nearest the periphery, where the osmotic action was first and strongest, show a removal of the nuclear content toward a central point. As one examines the cells that occur successively inside or central of this, it may be noticed that the results of osmotic action were less and less. In the central parts of the specimen no osmotic action is shown. The osmotic action produced by the alcohol has not moved the nuclear organs with reference to one another. In the specimen in question the plasmosome is clearly oriented with reference to the dorso-ventral line. No matter from which side the nuclear content has been compressed, the plasmosome is always clearly ventral in the compressed mass.

Torpedo ocellata, No. 22, 30 cm. long (large), killed with a knife and the entire brain fixed in Carnoy's fluid; absolute alcohol, chloroform, and glacial acetic acid, equal parts, the fluid being saturated with corrosive sublimate. This specimen showed about 85 per cent of its plasmosomes oriented ventrally, the remaining 15 per cent being scattered in median or somewhat dorsal positions.

Torpedo ocellata, No. 23, 30 cm. long (large), killed with knife and brain fixed in Carnoy's fluid; chloroform, absolute alcohol, and acetic acid, no sublimate being added. A fair fixation with 90 per cent of the plasmosomes ventrally oriented.

Torpedo ocellata, No. 24, 11 cm. long (small). This small fish was thrown whole into 60 per cent alcohol, containing 3.5 per cent of formol. It had given many shocks before being killed. No orientation in a ventral direction beyond a possible 5 per cent was found.

Torpedo ocellata, No. 25, 38 cm. long (large). This fish was left undisturbed in a tank for 48 hours and then gently lifted out on a tray, where it remained until dead. The brain was fixed in Bouin's fluid. 99 per cent of the plasmosomes were oriented sharply in a ventral direction. Chromosome bodies were somewhat clumped, owing to the natural death of the fish, the karyosomes standing out plainly and staining sharply and differently from the perichromatin.

Torpedo marmorata, No. 26, 16 cm. long (small). This fish was left undisturbed 48 hours and allowed to die on tray without discharging electricity. About 5 per cent of ventral orientation of the plasmosome was found.

Torpedo marmorata, No. 27, 11 cm. long (small). This small fish was irritated until considerable electricity had been discharged and then the brain-case was cut out while alive, the animal giving off strong shocks. After cutting sections the electric motor nerve-cells showed barely 5 per cent of ventral orientation, which appears to refute Magini's theory.

Torpedo ocellata, No. 28, 16 cm. long (small). This fish rested undisturbed for 48 hours and was allowed to die on tray. 10 per cent of ventral orientation.

Torpedo ocellata, No. 29, 11 cm. long (small). Caused to discharge freely and then killed by cutting out brain, with consequent strong shocks. No perceptible orientation.

Torpedo ocellata, No. 30, 40 cm. long (large). Kept for 48 hours at rest and then gently lifted from the water on a board and allowed to die without giving shocks. Brain fixed in Bouin's fluid. Sections in celloidin and paraffin show over 95 per cent of ventral orientation.

Table of experiments.

No. of specimens.	Length (cm.).	Mode of death.	Amount of orientation in control.	Gravity experiment.	Electric experiment.
1	15	Cutting; shocks before.	80 p. ct. ventral.	None.	None.
2	23	Chloroform.	65 p. ct. ventral.	None.	None.
3	30	Cutting.	75 p. ct. ventral.	543 times gravity, 2 minutes.	Electric current 110 volts weakened.
4	30	Cutting; shocks before.	70 p. ct. ventral.	828.5 times gravity caudad, 30 minutes.	110 volts, 4 mins.
5	35	Cutting.	Not examined.		110 volts.
6	30	Cutting.	Not examined.		4 volts, 1 hour.
7	12	Cutting; many shocks.	None.		4 volts, 1 hour.
8	11	Cutting; shocks before.	None.	Kept upside down 8 days, once gravity.	
9	16	Cutting; worried before; many shocks.	15 p. ct. ventral.	40.6 times gravity	None.
10	27	Cutting; few shocks.	5 p. ct. ventral.	Some cells studied alive under immersion.	Weakened current of 110 volts.
11	42	Cutting.	95 p. ct. ventral.	Live cells studied.	
12	30	Cutting very quickly; strong shocks.	25 p. ct. ventral.		
13	35	Cutting; shocks.	95 p. ct. ventral.		
14	30	Cutting; many shocks.	30 p. ct. ventral.		
15	38	Cutting; many shocks.	95 p. ct. ventral.		
16	42	Cutting; few shocks.	90 p. ct. ventral.		
17	32	Chloroform.	85 p. ct. ventral.		
18	30	Cutting; worried before.	90 p. ct. ventral.		
19	34	Died in air.	10 p. ct. ventral.		
20	37	Killed with knife.	10 p. ct. ventral.	601 times gravity, upside down, 30 minutes.	
21	35	Killed with knife; many shocks before.	95 p. ct. ventral.		
22	30	Killed with knife.	85 p. ct. ventral.		
23	30	Cutting; few shocks.	90 p. ct. ventral.		
24	11	Thrown in alcohol and formol; many strong shocks.	5 p. ct. ventral.		
25	38	Taken from rest and died on floor; no shocks.	99 p. ct. ventral.		
26	16	Died on floor; no shocks.	5 p. ct. ventral.		
27	11	Irritated, vivisected and brain cut out.	5 p. ct. ventral.		
28	16	Rested 48 hours; died on floor; no discharge.	10 p. ct. ventral.		
29	11	Irritated and brain cut out.	None.		
30	40	Died at rest on floor.	95 p. ct. ventral.		

The table on page 236 gives a summary of the list of the torpedoes experimented upon, with their sizes (length in centimeters), the mode of killing, and the amount of ventral orientation of the plasmosome in the nucleus, found in each case by counting 200 cells and estimating the percentage as follows: the nucleus was roughly divided by the eye into an upper and a lower half in each of the 200 cells counted. The number of cells with the plasmosome in the upper half (always smaller) was subtracted from the number with the plasmosome in the lower half and the percentage which this difference was of the entire 200 was assumed as the percentage of differentiation or ventral orientation in the specimens under consideration. This seemed to be a fairly accurate method for this purpose.

A few remarks must first be made as to the amount of "shocking" or electrical discharge performed by the fish under each method of killing. Cutting (vivisezione), as mentioned by Magini, was performed in 14 cases. This method was fairly quick, being hastened in order not to deliberately torture the fish to any great extent. It was considered by the writer that the usual stimulation, and teasing or worrying, which resulted in numerous strong shocks, produced as decided and characteristic physiological activity as that produced by torturing with the knife. However, even when killed by quick, deep slashes which cut the gills and the spinal cord and separated the upper brain from that part which bears the electric lobes, enough strong shocks were given to satisfy Magini's condition of "vivisezione," and when the fish was sharply teased, frightened, and worried before this until the shocks began to weaken, it appears certain to the writer that any visible material effects on the nerve-cells, due to an immediately previous large discharge of electricity, must become apparent.

As Magini has said, when a torpedo is allowed to rest in a tank and is then taken from the water very quickly and cautiously by slipping a dissecting board under it and raising it out and on to a table and leaving it there for several hours until death has ensued, then the fish dies without giving practically any shocks. This was found to be true in nearly all cases.

Poisoning the fish in any way was not a success, as with most poisons it gave electric discharges of considerable strength, but not enough to make one feel that the motor electric nerve-cells would show any effects. With chloroform the result was of particular interest because the fish remained quiescent under this drug, carefully administered, until all muscular action of the tail and fins had ceased. Then, in what the writer takes to be the critical period, when death finally arrives, the fish gave about 90 to 100 single, fairly strong shocks, each of which was spaced from the one preceding it and that succeeding it in a way that led him to believe each one to be correlated with a single heart-beat. No galvanometer was available to correctly portray this process, but it seemed from its "feel" that each shock was a single wave, one such as is portrayed on the plates prepared by physiologists in series to represent the intermittent current of the ordinary shock given by the fish.

We are now ready to take up and discuss the questions on pages 231 and 232 and see what the experiments show.

1. Is there an orientation of the plasmosome? A glance at the table, in the fourth column, will show that there is. Also that it is a more or less variable fact, in this torpedo reaching from some specimens in which no orientation appears up to specimens in which, as in our large American form, *Tetronarce occidentalis*, the percentage is about 100.

2. Is this orientation due to the immediate physiological activities which accompany nerve discharge? This certainly does not seem to be the case. Fish of all sizes were examined after being killed both by "vivisezione" and by being allowed to die without giving shocks, and the table shows that neither a condition of ventral orientation nor the reverse can be predicted by the method employed in killing or by the amount of activity shown by the fish's electric apparatus previously to the death of the specimen. In fact, strong negative and positive reasons exist which indicate the reverse of this, Magini's main contention. Twenty-five of the experiments were with fish that were killed by the knife. In many cases they were persuaded to give many shocks before being killed. In 2 cases all of the brain was used for other experiments, so that we have remaining 23 cases to consider and analyze.

In these 23 cases, Nos. 1, 3, 4, 6–16, 18, 20–24, 27, 29, and 30, we have all degrees of orientation, from less than 5 per cent in such cases as Nos. 9, 10, and 24 up through 10 per cent, 20 per cent, 70 per cent, and 85 per cent to a nearly perfect ventral orientation, as in the American *Tetronarce*. This clearly makes it impossible to agree with Magini in this regard, for we can not see in the table any consistent agreement between the amount of immediately previous physiological activity of the electric organ and the amount of ventral orientation of the plasmosome. Nos. 9, 24, 27, and 29 show fish that were forced to use the electric organ to excess just previous to death, and yet both showed only 5 per cent of ventral orientation of the plasmosome. Also, Nos. 7 and 8 were killed according to Magini's method, but they show no orientation.

Looking at the other side of this factor, we find on the list several fish which died quietly without using their electric apparatus to any extent before death. Again we find that a quiet, inactive death has not resulted in all cases in a lack of ventral orientation. No. 2 was chloroformed and shows 65 per cent; No. 19 died according to Magini's formula and happens to show only 10 per cent; but passing to Nos.

25 and 30, we find fish that were killed without electrical activity and show 99 and 95 per cent of ventral orientation respectively. Other experiments not recorded here have also shown that the fish which die quickly do not always show a general or central distribution of the plasmosomes.

The third condition can now be discussed, namely, that this orientation of the plasmosome is a permanent condition. To arrive at a conclusion it must be shown that there are no temporary movements of the plasmosomes during the electrical activity of the fish.

Fresh slices of the electric lobe were cut with a Valentine's knife in a vertical direction and after being covered and put under an immersion lens they were subjected to electrical and other stimuli that would have been sufficient to cause their discharge in a living fish. While thus being stimulated they were closely watched and it was noted that no movements of the plasmosomes occurred.

The fact that the plasmosomes exhibit a widely differing percentage of orientation in different individuals and that this percentage appears to be the same in all parts of the electric lobes of each individual might also seem to indicate that there were no temporary movements of the plasmosome. This has been further controlled by observing both fresh material as mentioned above and different fixations of the same specimen, after further stimulation followed by fixation and sectioning. Thus No. 10 was killed with the knife and fresh material was at once put under the microscope, where it was determined that the percentage of ventral orientation was 5 per cent. This was a very weak ventral orientation, so the remaining tissue, still capable of physiological action, was further stimulated both mechanically and electrically and then bits were fixed and sections cut. These preparations showed no futher orientation, so it was concluded that the excess stimulation had not moved them, and since this stimulation was applied to cells that were not ventrally oriented, and in which there was still room for orientation, this was considered to be strong proof that there is no ventral movement during the nerve activity which results in the electric discharge.

Another strong point must be considered at this time. Magini erroneously assumed that the functional axis of these cells lay in all cases in a dorso-ventral direction, with the implantation cone and neuraxis on the ventral side of the cell (text-fig. 4); and he therefore states in some places that the plasmosome (nucleolo) moves ventrally, and in other places he states that it moves toward the origin of the neuraxis. The writer, as stated in the description of the cells above (page 216), has found that a certain number of cells in each electric lobe, about 20 per cent of them, are so situated that the neuraxis leaves in a lateral or even in a dorsal direction (text-fig. 5), and that in these cases the plasmosome acts in accord with the majority of usual cases, *i. e.*, those with the axone leaving from the ventral surface. So that it may be stated that in cases of orientation the plasmosome is not oriented toward the axone or in the structural (physiological?) axis of the cell, but that it is always oriented in the dorso-ventral axis of the cell. Of course, the dorso-ventral axis *might* be a physiological axis, but its independence of the structural axis as formed by a line drawn through the majority of the dendrites, the nucleus, and the axone, would still require an explanation of why it was dorso-ventral. It could only exist in this direction to accommodate the factors of gravity or the electric current, and we shall see that in *Torpedo* it does not do this. It thus seems to the writer that the orientation, where found, is a more or less permanent condition, persisting over a considerable period of the animal's life.

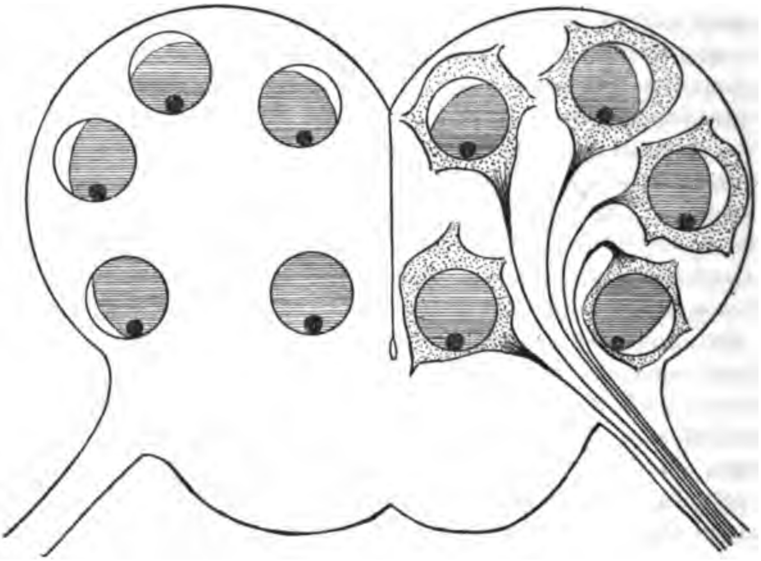


FIG. 5.—Diagram of form of electric lobes as seen in transverse section, with several enlarged outlines of a few cells on right that show how the neurite may arise from any surface of the cell and how the orientation of the plasmosome is always independent of this factor. Nuclei alone shown on left.

The fifth hypothesis, that this more or less permanent orientation is of value to the physiological activities of the cell, is a difficult one to discuss. Since it appears to be much more profitable to consider it in a paper on the more highly differentiated electric nerve-cell of *Tetronarce occidentalis* that is shortly to appear, it will be dismissed here with the remark that no strong evidence has been produced to show that such relation exists. Against it appear several facts:

First, the condition mentioned above, that the axis of orientation of the plasmosome does not correspond in all cases to the functional axis of the cell, would seem to indicate this. It might be assumed that any physiological action taking place in a definite direction would take place in the functional axis of the nerve-cell. Among such activities we would have to consider the movement of nuclear matter out of the nucleus into the cytoplasm to become or to help form the chromophyllic substance, the respiratory and nutritive processes connected with the discharge, and the performance of the discharge itself.

Again, and a stronger point, we find that in many fish, of all ages (or size), there is practically or actually no orientation at all. This would seem to settle the argument. It can not be a necessary condition of functional activity.

We now find ourselves ready to consider two possible immediate causes of the orientation, both of which are simple physical factors and are conditions affecting the cells only during the individual life of the animal. One of these is the electric current in which the cells lie at the time of each discharge of the electric organ, and the other is the force of gravity which, owing to the flat shape of the fish and its sluggish habits, exerts its power on the cells and all their parts in a definite direction during its entire life from birth on. We will consider the electric current first. It has already been explained about the fish's own current passing through the brain, but the writer may be pardoned for repeating this explanation with more detail at this point.

Cavendish (7) was the first to examine the different parts of the body of the torpedo and of its surrounding media and to plot a series of lines representing the courses taken by the electric currents that it generates (see text-figure 1).

Dubois-Reymond, working on the electric currents developed in connection with the shock given by *Malopterurus* (13), showed undoubtedly that the currents flow in part through the animal's body, and with a strength that is comparable to the currents developed in the surrounding medium.

Boll, in a very thorough research on the torpedoes (4), improved on Cavendish's work and showed the same electric-current lines that this author described in greater detail. The point to be noticed in his work in connection with this paper is that the current curves pass not only through the surrounding water, but a good part of them also pass through those parts of the fish's body that are not occupied by the electric organ. Owing to its position in the body, this is particularly true of the brain, including the electric motor ganglia, in which are the cells under discussion in this paper. (See text-figure 2.)

This means that during every discharge of a torpedo, given while under water, a current is passing downward through the brain or in the opposite direction to its course as generated in the electric organ itself. The question is: does this current, operating at intervals during the life-time of the animal, exert any influence on the plasmosome that would account for its orientation in those cases where orientation occurs?

Two methods of desirable experimentation presented themselves. One was to in some way reverse the natural current in order that it might pass in a reversed direction through the cells for some long period. This was found impracticable in the time at my disposal. The electric organs could not be reversed by an operation, owing to their large size and vital connections; still less could the brain-parts be displaced or operated upon. It was attempted to disconnect the electric organ from the brain by an incision which might cut the electric nerves and then to substitute an artificial current through the brain of strength equal to the natural one for considerable periods, but the fish all died, not being able to survive the operation. It is hoped in the future to be able to do this with an improved technique.

The second method was to excise portions of the electric lobes and to subject them while fresh and living to electrical currents of various kinds. This was done in 6 cases, Nos. 3, 4, 5, 6, 7, and 10. These results will now be considered.

The first experiments consisted in passing direct currents, of a strength approximately equal to that of the fish's own current as found passing through the brain, through the cells in question in a direction at right angles to the natural current and also in a reverse direction. It was not easy to estimate the strength of this current in the fish at the point where it passed through the brain, but a rough estimate was made and some small batteries were arranged so as to give an approximately equal current. This current was passed (torpedo No. 7) through a cylindrical bit of the electric tissue which was cut out of the electric lobes so as to be 4 mm. in diameter and 1 cm. long. This was placed in a glass tube and platinum electrodes were used to lead in the current. The tissue was cut so that its long axis was anterior-posterior or at right angles to the dorso-ventral line through which the natural current passes.

This experimental current was allowed to pass through the tissue for half an hour. Then the tissue was fixed and cut, but the sections agreed exactly with the control, so that the current made no change in the structure. Other currents of varying strength that approximated the natural current were used, some of them clearly as strong or stronger than the natural current. No. 6 was arranged so that the experimental current was in a direction reversed to the natural current. The time in this case was 1 hour, easily past the time during which the tissue lived. In both these cases no positive result was attained, and it seems to show that the plasmosome is not moved by these currents. Whether it would be moved by such currents if they were applied to it while it still lived, for weeks or months, can not be said. Currents of this sort which do not kill the tissue have been applied to plant cells by McClendon (25), also by Pentanalli (29), and to animal cells by Conklin (9) and Lillie (23).

Stronger direct currents were then tried by modifying the 110-volt current to a strength that "cooked" the tissue, and some interesting results were attained which as yet it has not been possible to interpret in an entirely satisfactory way. Nor did they seem to throw a very definite light upon the question of orientation. They probably, however, do give some basis for deduction and will be described. These experiments, in the order of the amount of current passed through the tissue, were on torpedoes Nos. 3, 10, 5, and 4. These four experiments resolve themselves rather easily into two types, the strong and the very strong current experiments. Torpedo No. 3 will represent the first and torpedo No. 5 the second. Exact measures of these currents are unfortunately lacking.

The first experiment (see fig. 19, plate 4) shows the following results: The outline of the entire cell was not changed in shape, nor were any of the processes modified. The nucleus was displaced bodily in the direction of the kathode, and its kathodal end, which was somewhat more than half of the whole nucleus, was considerably swollen, especially in a lateral (with reference to direction of current) direction. The anodal end was smaller and sharply set off from the other end by an inset that can best be seen in the figure.

The total displacement of the nucleus in the kathodal direction appears to have resulted in an almost vacant space on its anodal side, a space that corresponds to the original position of the nucleus in shape and size. This space is almost filled with a delicate clot which is thinnest and most delicate at its center, or next to the nucleus.

Bulging out from the anodal point of the nucleus is a very peculiar bag or sac-like structure with a sharp and somewhat flattened outline. It contains nothing in the sectioned and stained condition. Apparently it is the result of an electrolysis through the anodal end of the nuclear membrane and its bounding membrane appears to have been formerly a layer or part of the nuclear membrane, or else it is a new membrane formed by the material that has passed out of the nucleus. The shrinkage of the anodal half of the nucleus may be accounted for by the escape of some fluid constituent.

On the kathodal side of the nucleus a sector of the cytoplasm, whose sides radiate slightly from the two edges of the inset mentioned above, is filled with some deeper-staining material, not composed of visible granules. Between it and the surface of the nucleus one sees a narrow region which is thin in texture and does not stain readily.

Inside the nucleus we find that the anodal and contracted half of the nucleus is filled with a homogeneous mass of dark-staining material, which I take to be a modified form of the perichromatin. In this material the plasmosome and the several karyosomes are to be seen "floating." The karyosomes appear to be distributed very evenly through the dark-staining mass and not to either "float" or "sink" in it, but the plasmosome is always found on the kathodal surface of the perichromatin mass, and while it never touches nor sticks out of the surface, it does appear to press up in a way that makes a little mound of the perichromatin above it. Neither the plasmosome nor the karyosomes are changed in structure or size by treatment with currents of this strength.

The kathodal end of the nucleus contains a very fine reticulum of meshes, the fibrils of which pass largely in the line of the electric current. Sometimes, or even usually, these meshes appear to hold one of the karyosomes, which has therefore not been able to move toward the anode and join its fellows that are distributed very generally through the modified perichromatin mass. Two such cases are to be seen in one cell and one in the other cell pictured in figure 19, plate 4.

This kathodal reticulum grows denser toward the kathodal surface of the nucleus and appears to have in it very fine granules of a chromatic material, chromatic at least with regard to iron hematoxylin, but not quite so strongly to the carmines.

It will be interesting to draw a short comparison between the action of the electric current on this large, highly differentiated nucleus of the electric motor nerve-cell and the small nuclei of some of the surrounding connective-tissue cells. Such nuclei are seen in figure 19, plate 4, and in them one sees a rude approximation to the conditions seen in the nerve-cell. The chromatin has been moved toward the anode, but has not been melted or dissolved into a homogeneous median as in the electric nerve-cell. The chromatin masses are still more or less distinct and no large plasmosome is apparent. This comparison may serve as an index of the superior analytical conditions to be secured by experimenting electrically with a large, highly differentiated cell (such as this nerve-cell) rather than with smaller tissue-cells such as have usually been worked with.

As for the exact processes by which the nucleus of the electric motor nerve-cell has been so changed, there is room for difference of opinion. It is certain that a large part of it is purely physical and mechanical, as described by many writers, but in the present case there appear to have been chemical changes as well. The perichromatin seems certainly to have undergone some melting or solution of its finer particles (the perichromosomes) and a mixture of this with the nuclear fluid; also the reticulum in the kathodal half of the nucleus seems to be an entirely new structure chemically. Further, the chromatic material in this reticulum, as well as the deep-staining material in the kathodal sector of the cytoplasm, appear to be materials that do not differentiate from the rest of the cell under any other circumstances.

The main point, however, that we learn from this experiment, a result that is obtained by all repetitions, is that the plasmosome is not moved by this strong electric current all the way toward the kathode, a condition that would have to obtain if its orientation in nature were due to the natural electric current. It does, however, move part way there, as far as the dissolved chromatin mass extends. When one remembers that this chromatin mass extends throughout the nucleus under normal conditions, it seems possible that the electric current, when in proper strength, may tend to move the plasmosome in the kathodal direction, which is the direction of the orientation that we are discussing. This possibility, however, is not a strong one.

Having considered the results of strong electric currents, I will now compare with them some results obtained by what I shall call very strong currents, such as were used in experiments on torpedoes Nos. 5 and 4.

Figure 20, plate 4, from torpedo No. 5, will show these results satisfactorily, and it may be best studied by a simple comparison with the last figure (19, plate 4), which represents the effects of strong currents. The same strong trend of the nucleus toward the kathode with the resultant semilunar space on the anodal side of it is apparent. Also, the movement of the principal chromatic material in a homogeneous mass toward the anode. The same little "blister," probably containing a soluble constituent of the nuclear content that has been passed through the anodal surface of the nucleus, is to be seen and is even larger and better developed than with the strong current.

This specimen, being stained with iron hematoxylin, shows the kathodal collection of chromatic material which, as has already been stated, is particularly susceptible to this stain. It may also be noted that the neurosomes are shown by the fixation and stain and that a series of light-staining, elongate areas are to be seen in the cytoplasm.

Two marked differences are seen as a result of increased electric action: the anodal aggregation of chromatic material has been differentiated into a thinner, lighter-staining kathodal layer, and a main anodal body that contains the plasmosome and the regularly spaced karyosomes. These latter show the second marked difference. Each begins to swell up and acquire a vesicle-like form with a non-staining interior. This bubble-like swelling does not begin from the center, but from near one side of each karyosome, so that the resulting spherical shell has a lump on one side which represents the original mass. The writer has no explanation for this reaction.

Again, we find that our main point to be deducted from the examination of these very strong electric-current experiments is that the plasmosome is not moved all of the way toward the kathodal end of the nucleus, but that it is moved to the kathodal limit of the anodally segregated chromatin.

It having been concluded that the electric current was not a direct cause of the orientation, the question of gravity was taken up for consideration. As in the case of electricity, this force was applied to the cells, as a centrifugal force, in directions at right angles to the dorsoventral direction and also in the ventro-dorsal direction or the reverse of the natural pull of gravity. In practically all cases the proper controls were secured and it soon became apparent that this force might be the main cause of the orientation. By referring to the table it will be seen that 5 experiments were performed on torpedoes Nos. 8, 9, 3, 20, and 4. Also, it can be seen that the forces applied to the tissues were, in terms of gravity, for torpedo No. 8, 1 time gravity in reverse direction to nature for 8 days; for torpedo No. 9, 40.6 times gravity for 2 minutes at right angles to force of gravity in nature; for torpedo No. 3, 543 times gravity for 2 minutes at right angles to gravity in nature; for torpedo No. 20, 601 times gravity in reverse direction to nature for 30 minutes; for torpedo No. 4, 828 times gravity at right angles to nature for 30 minutes.

Thus we have a series of 5 experiments ranging from the natural force of gravity reversed and applied for 8 days up to 828 times gravity applied for 30 minutes.

The first experiment of this series, on torpedo No. 8, yielded no visible results. In this case we had a small fish to deal with, which somewhat lessens the value of the experiment. No orientation appeared in the brain as a result. Thus the questions are left open: Did any orientation exist in a ventral direction which had been nullified by the experiment? And, would a result have appeared if the fish were larger and had possessed a natural orientation? Another experiment of this nature should have been tried on a larger fish, but the two questions can still be answered, I think: the first by the statement that all small fish possess no orientation, or very little, and the second by a similar experiment performed on an adult *Tetronarce occidentalis*, to be described in another paper, in which the plasmosomes are always oriented sharply in the ventral position. The same experiment performed on this large fish showed that gravity alone could not move the plasmosome in 7 days in this adult form.

Turning to experiments on torpedo No. 9, we find that we are dealing with a 16 cm. fish, which is small, but not as small as torpedo No. 8. The control made in this case shows that a considerable amount of natural orientation was present, about 15 per cent. The force applied as a centrifugal force by the centrifuge was low compared to the later experiments, but high compared to gravity, being a little over 40 times that measure. The time was 2 minutes and perhaps should have been longer to show a complete negation; still, since some of the later experiments with stronger forces were also of short duration, we can feel satisfied that real results are being secured and real comparisons being made. The results in this example were completely negative, showing that when 40 times the force of gravity is applied for 2 minutes the contents of the nucleus remain undisturbed.

The next experiment, on torpedo No. 3, was positive in its results. The force used was 543 times gravity for 1 minute. The plasmosomes were all moved by an anterior-posterior centrifugal force of this strength from varying positions, mostly ventral, to a position in a posterior arc of about 40 degrees. (See text-figure 6, *zg*.) In this arc the nuclear wall is so flat with respect to the direction of the force exerted that it makes very little difference in what portion of such an arc a plasmosome comes to rest, just as the natural force of orientation always brings it into the arc *xy* (text-fig. 6), but into any part of that arc. Thus, in text-figure 6, we have a diagram representing the outline of a nucleus of one of the electric motor nerve-cells with one arrow representing the direction of the force of gravity and another representing the centrifugal force as applied in this experiment on No. 3, as well as in other experiments where greater forces were employed. In such a cell the normal position of a naturally oriented plasmosome is at 1-*a*, although it may rest in any part of the arc *xy*, as at 1-*b* or 1-*c*. When centrifugal force is applied of sufficient extent to change the position of the plasmosome it moves in the direction indicated by the two-barbed arrow until it comes to rest on the arc *zg*. If the plasmosome starts from 1-*a*, or even from a more dorsal position, as 3-*a*, it will come to rest well in the ventral part of the arc *zg* or at 2-*a*. In this case it rolls along the curved outline of the nucleus until the first part of the arc is reached at *g*, when it stops because the angle is too obtuse. If it starts from a median position, as at 3-*b*, or from any position on a median line with reference to the centrifugal force applied, as at 3-*e* or 3-*f*, it will come to rest in the center of the arc *zg* at 2-*b*. If it lies in the dorsal half of the nucleus as at 3-*d* or 3-*c* it will be located by the centrifugal force at 2-*c*.

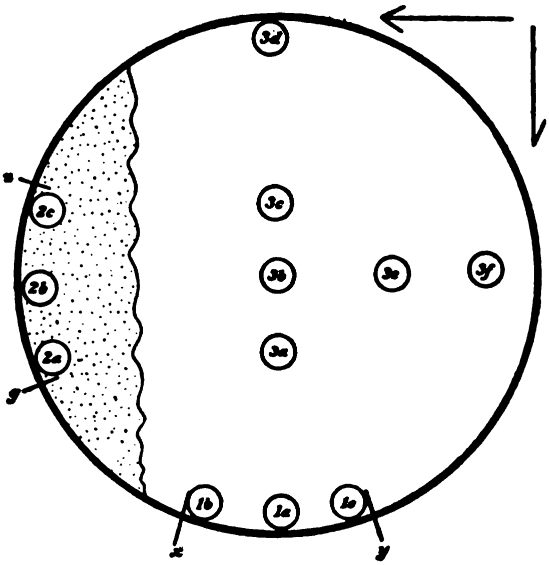


Fig. 6.—Diagram showing arc in which the plasmosome will not move when it arrives from any part of the nucleus.

Thus it becomes very easy to estimate the percentage of the central orientation of the plasmosome, even after centrifugal force has been applied at right angles to gravity and the plasmosome has been reoriented by this new factor. Ventrally oriented plasmosomes will become located in the ventral portion of the centrifuged mass of chromatic material as indicated in text-figure 6.

It was very noticeable that only the plasmosome was moved and that the other structures in the nucleus appeared to maintain their positions. In some few cases a few of the chromatin bodies seemed to be moved from their position with relation to the other bodies in the nucleus, but for the most they were not disturbed. Figure 21, plate 5, shows one of these cells.

An interesting cytoplasmic change took place in this specimen, which may be mentioned here. The whole nucleus, as well as the cell itself, appeared in a number of cases to be slightly flattened by the pressure, and as a result a circular equatorial channel filled with lymph-like fluid appeared to girdle the nucleus. From this belt-like channel a series of radiating lines of some form of non-staining cytoplasm pass out. They are not fibrillar in nature and the whole structure simulates superficially a centrosome. This torpedo was of large size.

In the next gravity experiment, on torpedo No. 20, a force of 601 times gravity was applied for a period of nearly half an hour. The control showed 90 per cent ventral orientation, as might be expected in so large a fish (37 cm.). As has been related in the account of the experiment, the force was applied in a ventro-dorsal direction, with the result that not only the plasmosome but all of the chromatin bodies were thrown against the dorsal wall of the nucleus. The plasmosome lay nearest to and against the nuclear wall. The chromatin bodies lay in a mass with its level inner edge forming a secant of the circular outline of the nucleus. It was noticeable that the chromatin bodies showed no signs of flattening and that the central body or karyosome had not moved through the perichromatin; the whole structures (chromatin bodies) thus appear to be bodies of considerable firmness. Nor were the entire chromatin bodies very closely packed; they still retained their round outlines.

A question suggests itself here: does the plasmosome yield to increasing centrifugal force first because it is not so strongly held as the chromatin bodies or because it is actually heavier? This can be answered, I think, from an inspection of the control or normal material. In such sections (see fig. 2, plate 1, and figs. 4 to 9, plate 2) one can easily see that the plasmosome is connected with all parts of the nuclear wall by a considerable number of strands of loosely woven fibrils and is evidently held in its position in the nucleus by as strong if not a stronger set of structures than are the chromatin bodies.

The last experiment of the gravity kind to be considered is that performed on torpedo No. 4, in which a force of 828.5 times gravity was applied by centrifuging a portion of the electric lobes in a direction at right angles to the natural force (anterior-posterior). The proportion of ventral orientation in the control was 70 per cent and with the large artificial force applied the entire number of chromatin bodies as well as the plasmosome were thrown against the posterior wall of the nucleus.

The general results were in a large measure like those found in the preceding experiment (see fig. 23, plate 5). A careful comparison of the two experiments will show such difference as came out.

The plasmosome was evidently thrown down with greater force. In many cases it dented the nuclear membrane. As in all other cases, however, it was not in the exact center of the thrown-down mass, but occupied one corner, the central corner, in a proportion of the cases that corresponded fairly well with the percentage of orientation, 70 per cent. The shape of the plasmosome was in no way changed, except in a few cases which might well have been caused by the fixative.

More of a change than this appeared, however, in the chromatin bodies. These structures had been flattened somewhat in most cases and in some cases were much flattened. The flattening, in all cases, was seen only in the perichromosomes and no signs of such a condition were visible in the karyosomes. These objects had not only retained their shape, but were also always in the center of the flattened chromatin bodies, as being in this case the center of an oval instead of a circular mass. It was also true that the mass of perichromatin was in most instances much smaller than in the control, and this appeared to be due to a loss of some part of the material rather than to its compression. However, the same phenomenon is often true in normal specimens, where it appears to be a result of certain fixations.

Another varying condition in this specimen, as well as in torpedo No. 20, was seen in the achromatic portion of the nuclear content. This material has usually been figured and described as a reticulum of some kind with a more fluid material, the "nuclear sap," in its meshes; and it does so appear in most of the nuclei of the motor electric nerve-cells of *Torpedo*, as seen in mounted sections under the microscope. The variation as noticed here consisted in the sizes of the meshes of the reticulum. Some showed a coarse meshwork and others a very fine one, with all intermediate sizes of mesh to be seen in the specimen. This reticulum has been considered by many investigators to be an artifact in part or in whole, and in particular the researches of Kite and Chambers and others show that, in the living cell, no such network of fine fibrils exists in reality. In the torpedo's electric motor nerve-cell this reticulum is clearly shown to be an artificial condition by the fact that with most of our standard fixations the outer layers of cells in a mass of fixed tissue show a finer reticulum in the nucleus, while the inner cells in the same bit of tissue show a coarser pattern.

This reticulum is not an alveolum, in that its various cavities break into one another at frequent intervals. It is a real reticulum, but not one composed of thin threads. Rather it appears to be such a reticulum as would be formed if the dividing walls of an alveolum were to be broken or punctured through at frequent intervals. Its varying patterns needed explanation and some teased fresh cells were put between cover-glass and slide and Flemming and other fixatives were run in under a 2 mm. apochromatic immersion lens with the best condition of lighting.

According to many investigators (Kite (22), Chambers, etc.), the achromatic contents of the nucleus during life are a thin colloidal sol which sometimes approaches a delicate gel in consistency. In the present case the writer has rather hurriedly dissected the nucleus under the Barbour apparatus and noted that it is a viscous gel, which is very soft and almost a sol in its fluidity. No traces could be observed of any fibrillation, either by an optical examination or by a physical examination with the glass needles.

This viscous fluid was carefully watched as the fixing fluid came in contact with it, and the following process seemed to take place: The fixative (Flemming's fluid seemed to give the best picture) advanced slowly on a more or less straight front with a fairly definite line between the portion that it had invaded and the parts as yet untouched. It seems probable that this fluid with its dense content of salts advances by a combination of an osmotic action and a mechanical rupture of the fixed wall that is always in front of it. The line of division mentioned above was seen to bend into a series of rounded pockets, which were broken inward by the increasing osmotic pressure and convection currents of the fixative burst into the unfixed mass of nuclear material. They fixed the new surfaces thus brought into contact with them, and then the process of bending inward portions of the new line of contact by osmotic pressure and again breaking through to form new cavities was resumed. As the fixative penetrates further, it becomes diluted and less vigorous in its action, and the united osmotic action of its salts on the line of contact becomes less. Consequently a larger portion of the line is bent in and broken, the successive pockets of inruption become greater, and the resulting mesh becomes larger, as seen in the fixed specimen.

In fixation by gases, such as by formol and by osmic-acid vapor, the penetration is by diffusion and the mechanical factor does not enter into the process. Also, in fixation by many fluids the diffusion of gases proceeds ahead of the osmotic-pressure action and we have nuclei whose contents are apparently homogeneous.

It can be seen that this combined chemical and mechanical action would account for the coagula that have been described for many body fluids and which are so characteristic for the blood and lymph fluids of many animals. An examination of such a coagulum is sufficient in many cases for an expert histologist or pathologist to state what fluid it is, what fixation has been used, and how far the cell or tissue examined was from the surface of the bit of tissue that was fixed.

One further experiment was tried, to throw light on the point of issue between Magini and Coggi as to the meaning of the dorsal meniscus seen by Magini in several cases and ascribed by him to the physiological activity of the cell. Coggi contended that this space was due to the strong osmotic action between a fixing fluid and the fluids of the cell.

The experiment performed by the writer was to place a brain of *Torpedo ocellata* (No. 21) in some light fluid, 95 per cent alcohol being used. This fixed the tissues, and when sections were cut it was found that the osmotic action had forced all the contents of each nucleus in a centripetal direction, leaving the spaces described by Magini on the outer side. These meniscoidal spaces are not outside of the nucleus, however, but are formed within its nuclear membrane, which retains its rounded shape. All contents of the nucleus take part in the movement, leaving an absolutely vacant space to form the meniscus.

As text-figure 5 will show, this action is centripetal with reference to the mass of the brain, so that laterally placed cells have the meniscus on their outer lateral side and some placed on the under side of the edge of the lobe have it placed nearly on the ventral side. Magini overlooked these fewer exceptions to the general conditions when he stated that the meniscus was always placed dorsally, in addition to his mistake of assuming that the neurite always left the cell in a ventral direction and that the physiological action of the cell as described by him was dorso-ventral in direction.

SUMMARY AND CONCLUSIONS.

The net result of the three gravity experiments on torpedoes Nos. 3, 4, and 20 seems to show that the plasmosome is the heaviest body in the nucleus, undoubtedly heavier in actual weight than the chromatin bodies and probably of a greater specific weight than any of the other nuclear organs, with the possible exception of the karyosomes. In young fish this plasmosome seems to have a central or general distribution, while in older or larger fish it acquires a constantly increasing ventral orientation, which the writer believes *due to its increasing size and weight*, together with a less resistant condition of the nuclear content to its slow movement through its mass. It may be said (and the observations, as shown in the table, bear it out) that in the small specimens of *Torpedo* under 12 cm. in length, nearly all cases show no orientation. From 12 cm. up a slowly increasing and quite irregular orientation in the ventral direction takes place, due to the increasing weight of the plasmosome, and greater or less in amount according to the resistance to its movement offered by the physical condition of the nuclear content. This content must be very slightly modified in its solidity, viscosity, etc., by food, by depth and water-pressure, and by individual variation. Such modification, however slight, would account for the variation in the amount of orientation found in different fully grown fish.

Such movement of the plasmosome must depend largely upon growth changes and readjustment in the nucleus which favor its passage through the achromatin. It certainly takes place very slowly, as can be inferred by examining the table of experiments, and the irregularity and slowness of the process seem to confirm the hypothesis that it is not a vital factor but a sort of by-product or accidental and unimportant feature of the development of this cell.

Magini's observations may be assumed to be correct, but the misfortune of finding an orientation in the fish that he vivisected and none in those which had been allowed to die without a strong previous use of the electric organs led him to formulate an incorrect if attractive theory. His further statements concerning the meniscoidal spaces at the dorsal side of the nucleus after great electrical activity were incorrect, as it was osmotic action that caused this condition—the action of either the fixatives or the subsequent alcohols.

The part played by the electric current in the physiology of this cell is probably negligible. While very strong currents did move the plasmosome or appear to control its position to a limited degree, the weak currents did not seem to influence it in any way. Gravity thus seems to be the cause of the orientation in question, which is not accomplished in this fish until later adult life, and is then a more or less variable factor of its structure.

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EXPLANATION OF PLATES.

All figures represent parts or the whole of electric motor nerve-cells from either *Torpedo marmorata* or *Torpedo ocellata*, which the writer believes to interbreed and to be structurally the same.

Magnifications are not given, because absolute measurements of the average cell are given in the text.

Where the results of experiments are shown the natural direction of gravity and the natural direction of the electric current are indicated by an arrow with one barb, while the applied centrifugal force and the applied experimental current are indicated by an arrow with two barbs.

PLATE 1.

FIG. 1. A normal cell from *Torpedo marmorata*, No. 16. Fixed in Bouin's fluid to which 5 per cent potassium bichromate was added. Iron hematoxylin. Shows large and numerous spindle-shaped chromophyllic bodies; also smaller, round, and deeper-stained neurosomes situated between chromophyllic bodies. One large and one small plasmosome. No telonucleolus. Typical chromatin bodies.

FIG. 2. A normal cell from *Torpedo ocellata*, No. 1. Bouin fixation. Cut in celloidin after bulk-staining with borax carmine and hemalum. One large and one small plasmosome. The small plasmosome lies inside of a telonucleolus. Several elongate and darker-staining nerve-sheath nuclei outside of cell; also three larger, rounder, and lighter-staining neuroglia-cell nuclei.

PLATE 2.

FIG. 3. A living cell from *Torpedo marmorata*, No. 16, seen with 2 mm. apochromatic objective, under very slight pressure of cover-glass and with iris diaphragm well cut down to bring out refractive properties of cell-structures. Plasmosome, karyosomes, nuclear membrane, and neurosomes sharply brought out. Perichromosomes slightly brought out, and cytoplasm granules around nuclear membrane weakly brought out. Some trace of chromophyllic bodies to be seen; also of neurofibrils.

FIGS. 4, 5, 6, 7, 8, and 9, nuclei from cells of several torpedoes, to show different arrangements of plasmosomes and of telonucleolus when present.

PLATE 3.

FIGS. 10 to 18. A series of cells from *Torpedo marmorata*, No. 16. Macerated for 3 hours in one-third alcohol and teased in very weak glycerin on slide. Distribution and color of neurosomes well shown. Form of individual neurosomes not well shown, as only masses of them appear. The functional polarity of the cell well known. Dendrites tend to gather at one end or pole and neurite with heaviest masses of neurosomes at the other. Cells do not lie in natural relative positions in plate, as selected specimens were drawn from different slides.

PLATE 4.

FIG. 19. Two cells from a section of the electric lobe of *Torpedo ocellata*, No. 3, through which a current was run from left (anode) to right (kathode). These cells show the general pressure on the entire nucleus in the kathodal direction, which appears to result in the appearance of the semilunar space on the anodal side. The other changes as described in the text.

FIG. 20. A single cell from the electric lobe of *Torpedo ocellata*, No. 5, to which a very strong current has been applied for 30 seconds from left (anode) to right (kathode). Fixed in sublimate, stained in iron hematoxylin. Shows increased results over preceding experiments. For description see text.

PLATE 5.

FIG. 21. A cell from *Torpedo ocellata*, No. 3, that has been subjected to a centrifugal force of 543 times gravity for one minute. Nucleus somewhat compressed and an equatorial canal formed. Plasmosomes alone moved by the force. Bouin fixation.

FIG. 22. A cell from *Torpedo ocellata*, No. 20, which has been subjected to a force of 601 times gravity for about half an hour and in a ventro-dorsal direction. Both plasmosome

and chromatin bodies moved by this force against dorsal side of nucleus. Coarse linin reticulum due to cell being situated in interior of specimen. Bouin fixation.

FIG. 23. A cell from *Torpedo marmorata*, No. 4, which has been subjected to a centrifugal force of 828.5 gravity in the anterior-posterior direction for 30 minutes. Both plasmosome and chromatin bodies have been thrown to the caudal side of the nucleus. Flemming's fixation. The perichromatin has been partly dissolved by the fixative, thus making the chromatin bodies smaller; and the fine linin reticulum indicates that this cell lay very near to the surface of the bit of tissue that was thrown into the fixative.

PLATE 6.

FIG. 24. General view, with partial dissection, of upper surface of *Torpedo marmorata*. Shows the two lateral electric organs and the brain with its electric lobes lying centrally between the electric organs. After Fritsch.

FIG. 25. Vertical, transverse section taken through fish seen in fig. 24. Shows the two lateral electric organs with their vertical column of flat disks, the electroplaxes, and the brain, cut in the region of the electric lobes, lying between the electric organs. The polarity of the E. M. F. generated in the electric organs is indicated by the plus and minus signs.

FIG. 26. Transverse section through medulla oblongata of *Torpedo marmorata*. The section passes through the thickest part of the electric lobes, whose large motor nerve-cells are seen to compose the greater part of its mass. The nerve processes of these cells are seen to be leaving the lobes laterally as the large electric nerves that go to the electric organ. After Fritsch.

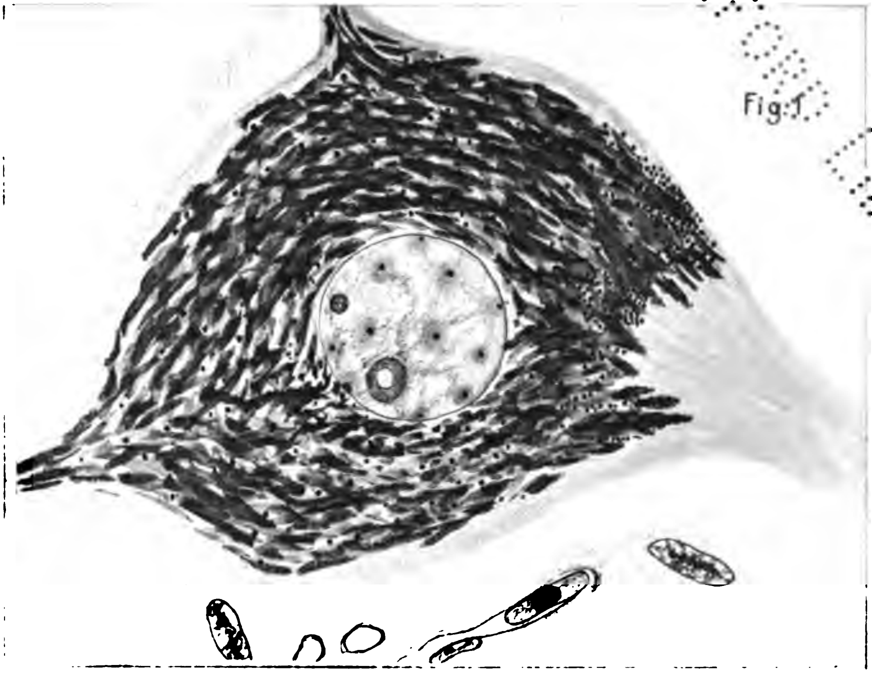

Fig. 1.

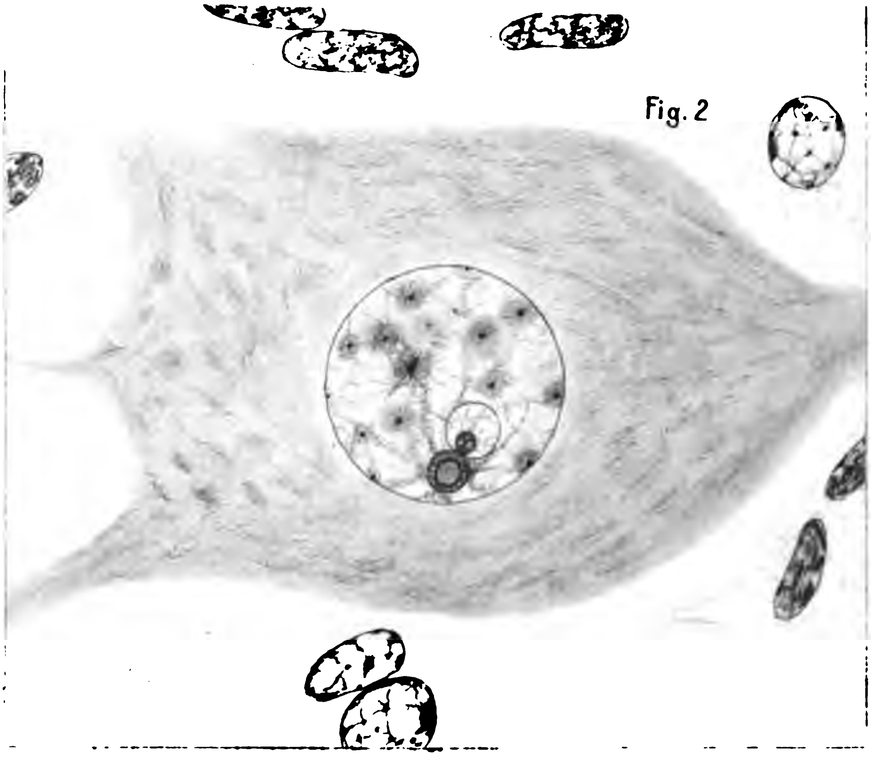

Fig. 2

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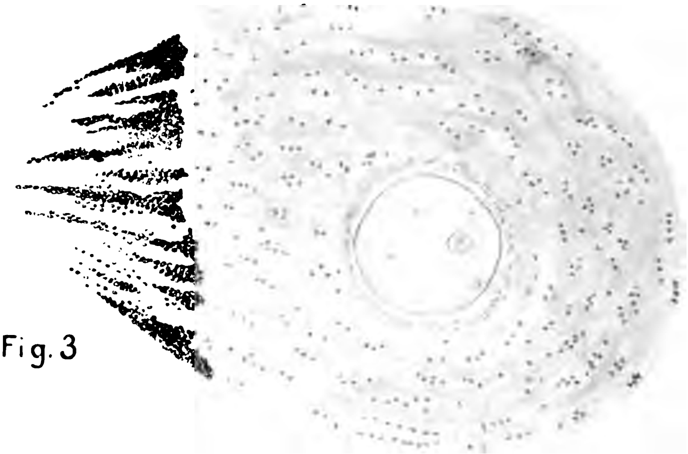
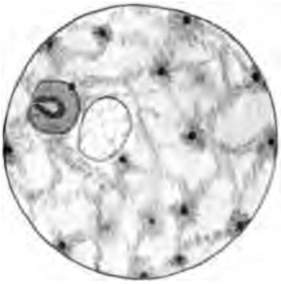


Fig. 3



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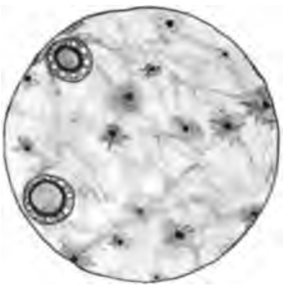

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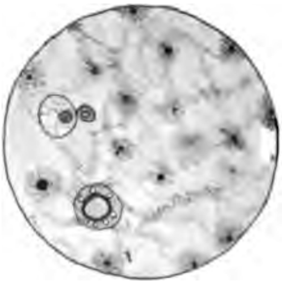

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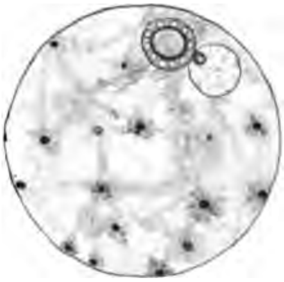

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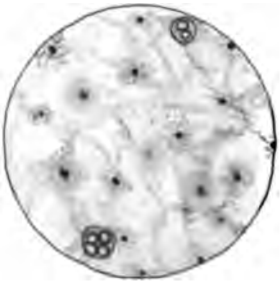

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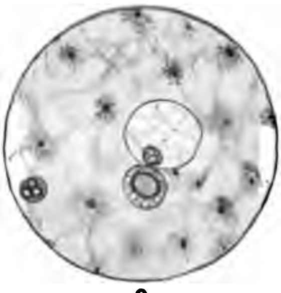

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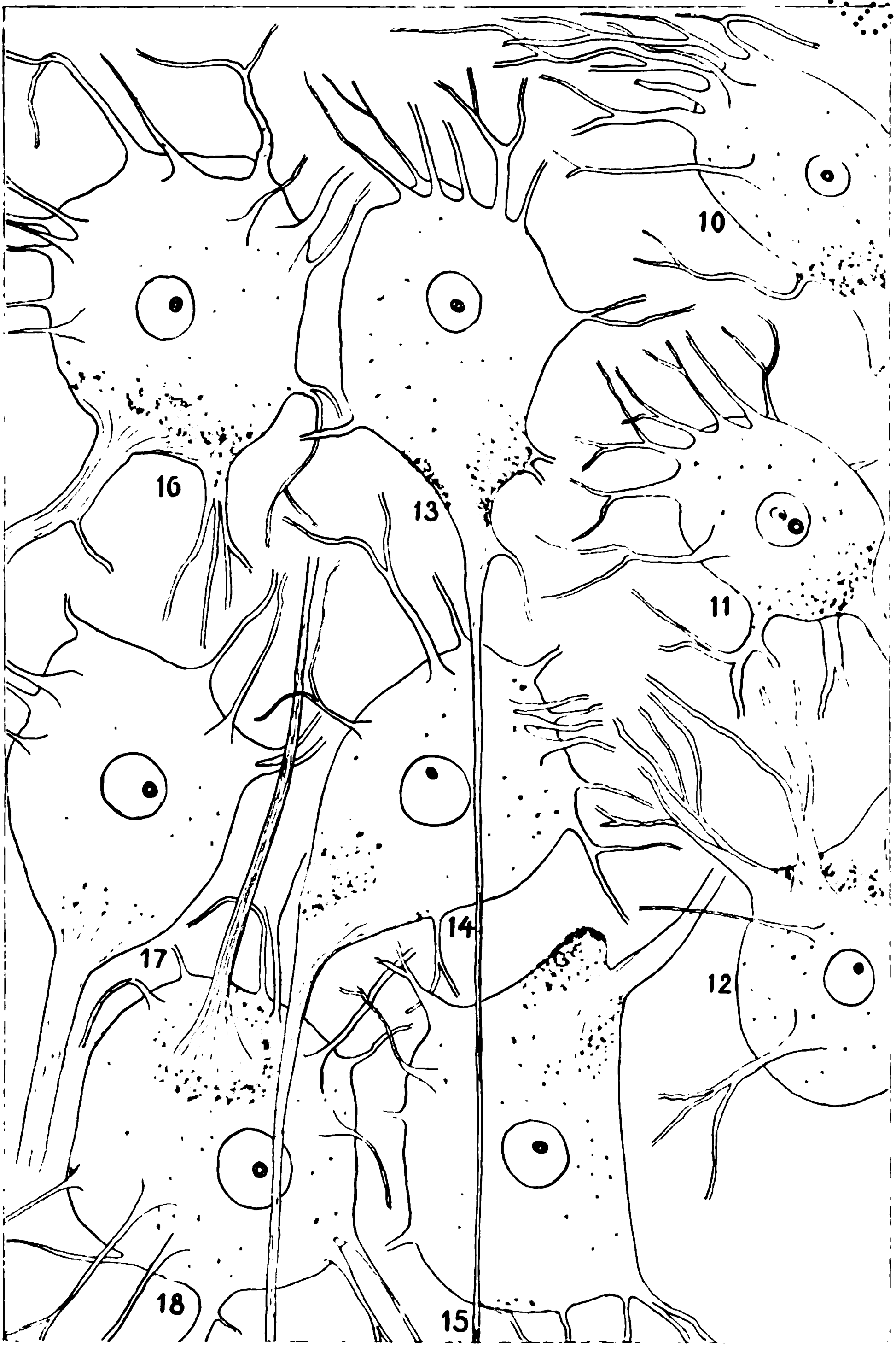
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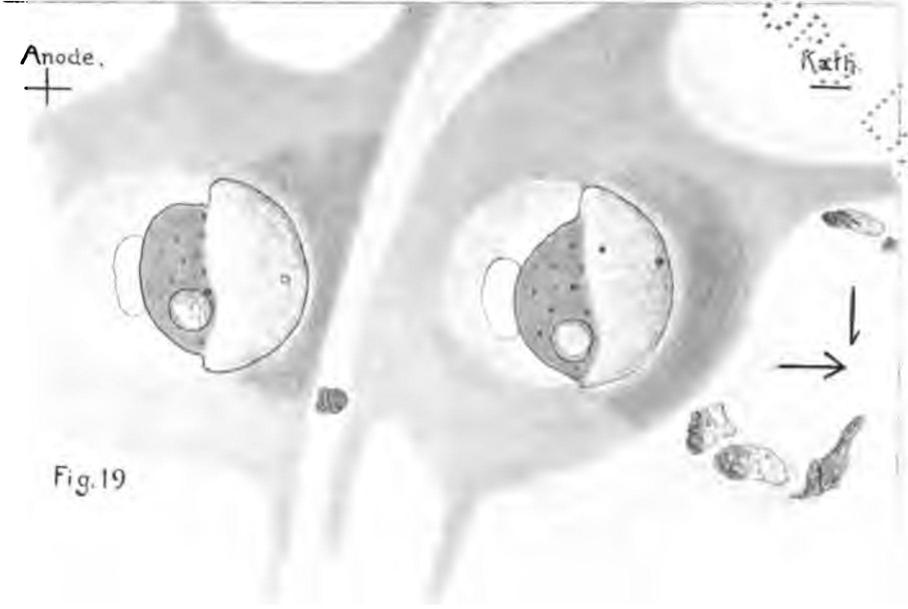

Fig. 19

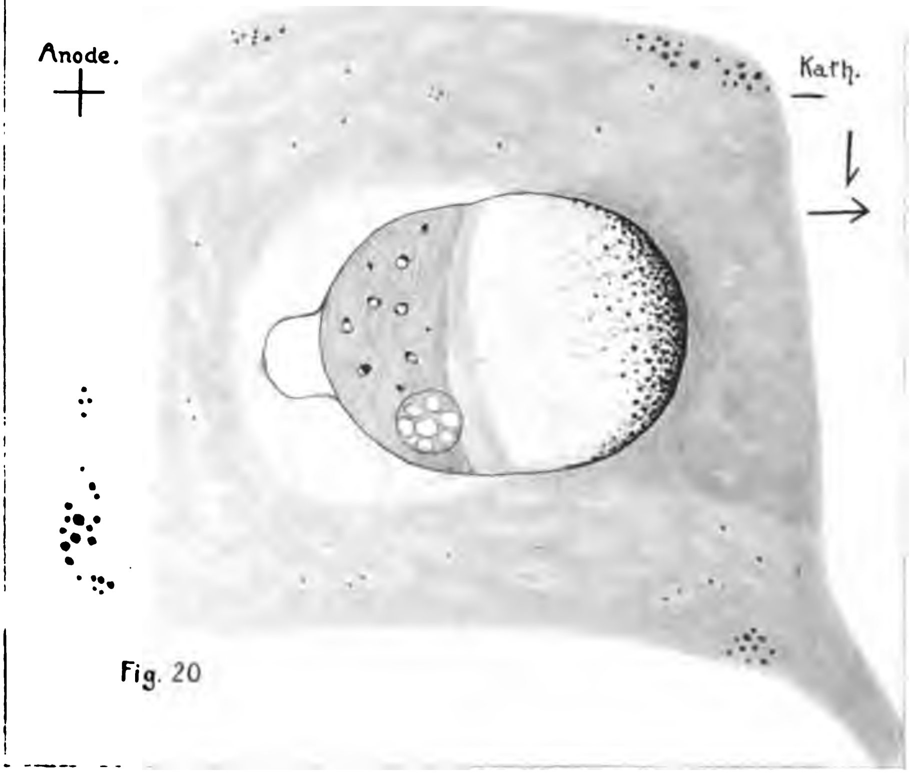

Fig. 20

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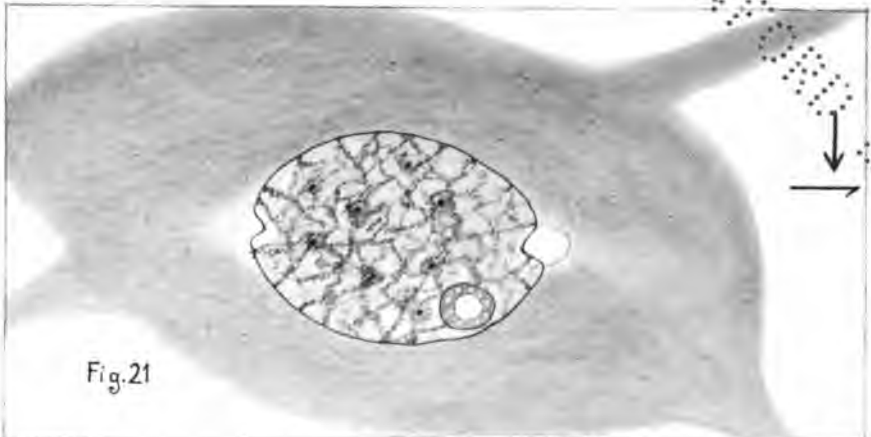

Fig. 21

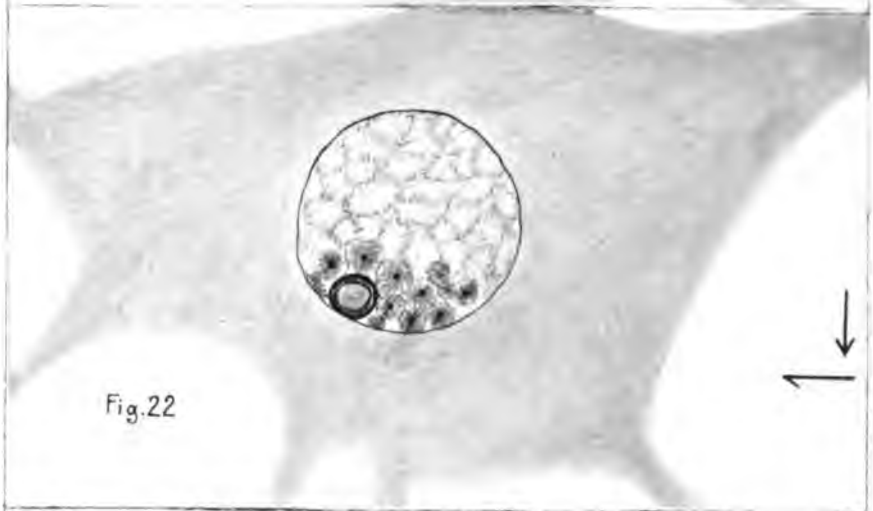

Fig. 22

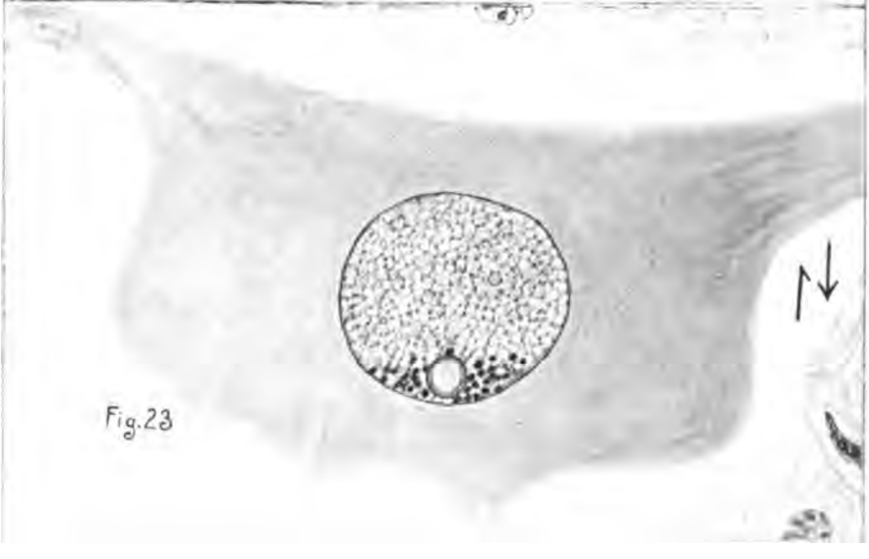

Fig. 23

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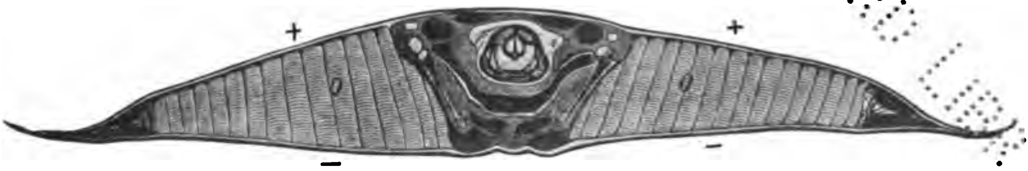


Fig. 25.

Fig. 24.—General view, with partial dissection, of upper surface of *Torpedo marmorata*. Shows the two lateral electric organs and the brain with its electric lobes lying centrally between the electric organs. After Fritsch.

Fig. 25.—Vertical, transverse section taken through fish seen in fig. 24. Shows the two lateral electric organs with their vertical column of flat disks, the electroplaxes, and the brain, cut in the region of the electric lobes, lying between the electric organs. The polarity of the E. M. F. generated in the electric organs is indicated by the plus and minus signs.

Fig. 26.—Transverse section through medulla oblongata of *Torpedo marmorata*. The section passes through the thickest part of the electric lobes, whose large motor nerve-cells are seen to compose the greater part of its mass. The nerve processes of these cells are seen to be leaving the lobes laterally as the large electric nerves that go to the electric organ. After Fritsch.

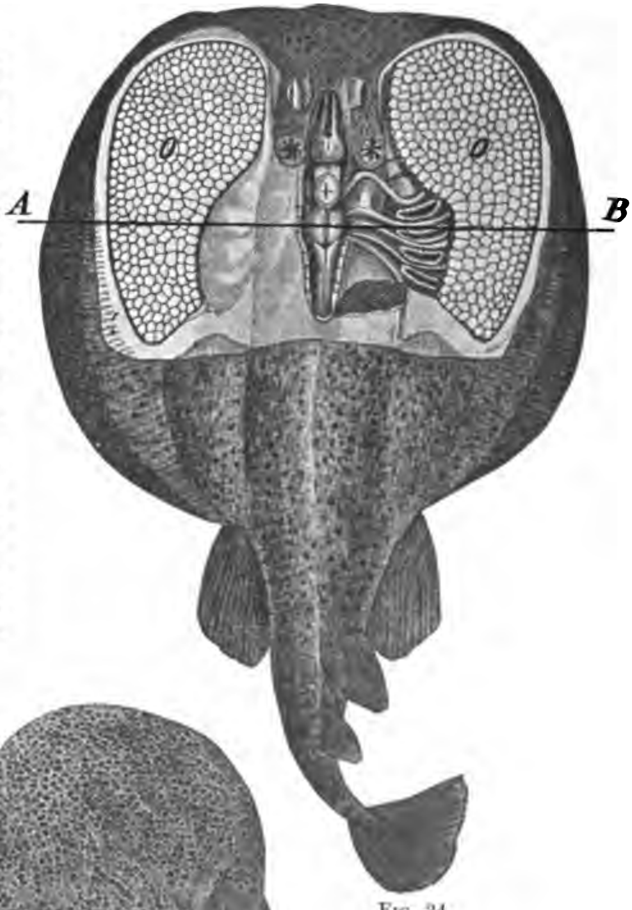


Fig. 24.

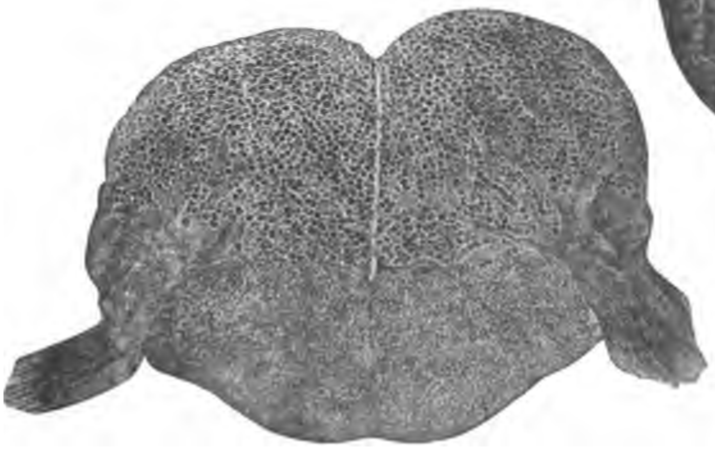
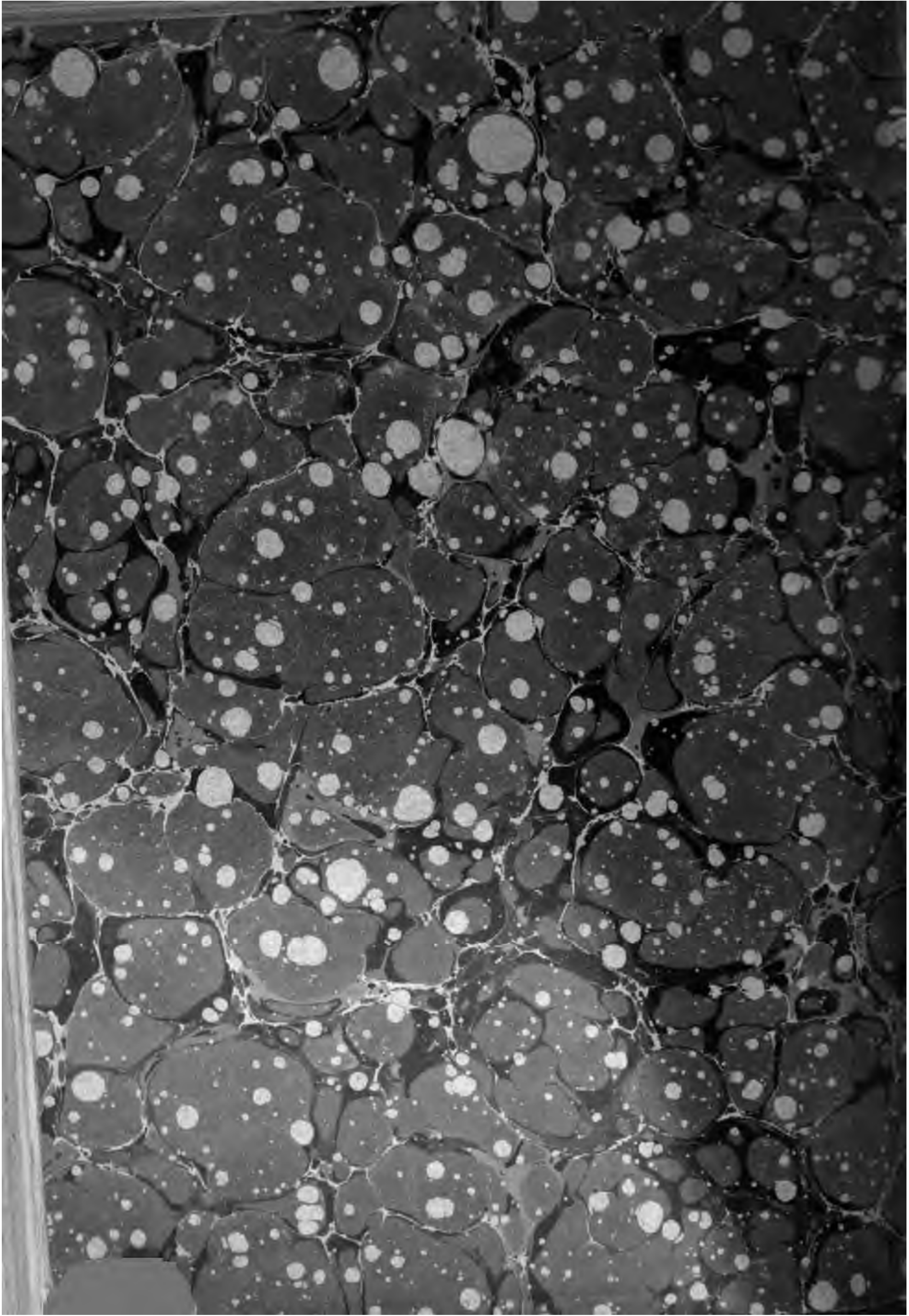


Fig. 26.



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